ACORNS IN HUMAN SUBSISTENCE

by

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ABSTRACT

The aim of the thesis is to examine the use of acorns in human subsistence and to relate this to the interpretation of acorn remains from archaeological sites.

The worldwide archaeological record of acorn finds is first reviewed, and archaeologists' interpretations of past uses of acorns are discussed. The ethnographic record of acorn use is next examined, with emphasis on similarity and variability within and between regions. Particular attention is paid to food-processing and detoxification techniques. An examination of the biological and ecological characteristics of acorns and oak trees follows, with emphasis on those factors which make them a useful resource, and, conversely, those factors which might bias against their use. Factors affecting the availability of acorns, and their nutritional qualities are considered.

Interpretations which have been made in the archaeological literature about acorn use are then re-examined in the light of the available archaeological, ethnographic, and biological data. Problems with the nature of the available data, and their use, are discussed, and the potential for a more critical approach to the use and interpretation of such sources of data is examined. Consideration is given to the extent to which taphonomic factors, relating to either cultural or natural processes, may influence the representation and interpretation of acorns in archaeological sites. Finally, the implications that the study of one potentially important wild plant-food resource may have for general models of past human subsistence are discussed.

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CHAPTER 1. INTRODUCTION AND AIMS

Much of the theoretical approach to archaeobotanical studies is grounded in concepts regarding the role of plants in human life, often with regard to subsistence, and specifically subsistence change over time. There is often a particular emphasis on the emergence, development and spread of agriculture. Various approaches have been summarised by Harris (1989), all of which make some distinction between subsistence based principally on the use of wild plants and that based principally on the use of domesticated plants. Harris himself provides a model of a continuum of people-plant interaction which is effectively a distillation of much of the thought on these lines over the last 30 or so years. As he says (p.22) "if the model is to prove useful in investigating the actual history and prehistory of plant exploitation...more comprehensive means than we have at present will have to be devised to trace in the archaeological record the range of plant-exploitative activities that make up the continuum". Harris goes on to review various archaeological techniques that may be useful in future in detecting activities indicated along the continuum which may have occurred in the past. However, as he suggests, many of them are as yet difficult to implement.

An alternative way of approaching such models might be to examine differences in the use of a resource which can be incorporated in a subsistence strategy falling anywhere along the continuum. This would ideally be a potentially staple resource, for which there is archaeological evidence over a wide range of areas and times, and for which there exists considerable ethnographic data. In terms of plant foods the main groups of potential resources are roots and tubers; the small, often starchy, seeds usually of annual plants; or the large nuts of trees and shrubs (Harris 1977).

As yet there is little archaeological evidence relating to the roots and tubers. The small seeds, of grasses in particular, offer much potential. Those grasses incorporated in wild-food procurement systems are (obviously) wild species, while those used in agricultural systems are predominantly domesticated species. This has many advantages in the archaeobotanical study of subsistence change, in that there is the potential for detecting change in the system via evolutionary transformation in the nature of the species involved. However, as models of subsistence change (at least those concerned with transitions to agriculture) are implicitly based on such transformations there is a danger of producing self-fulfilling prophecies when using such resources to 'test' such models. Of the three types of plant-food resource then, the tree nuts hold a potential which has seldom been considered in general models of subsistence change, largely <u>because</u> they have not generally undergone the same kinds of evolutionary changes - or come to occupy roles as

domesticated staples within agricultural systems - that roots and tubers or annual seed plants, have; probably for good biological reasons (Harris 1977).

There are several fairly widespread genera of trees in the temperate zone which produce edible "nuts", including *Castanea* (chestnuts), *Corylus* (hazelnuts), *Fagus* (beechnuts), *Juglans* (walnuts) and *Pinus* (pinenuts), as well as various members of the Rosaceae. The genus *Quercus* has numerous species and is widely distributed through much of the temperate zone, and beyond. Acorn remains have been recovered from archaeological sites throughout much of their range of distribution. There is also a widespread, and often detailed, ethnographic record relating to the use of acorns. In addition, acorns are nutritionally closer to the ideal of a "staple" food (as represented by the annual seeds and roots and tubers) than most other nuts, being principally a source of carbohydrate.

The wide range of ethnographic data on acorns has particular advantages in relation to examining models of general subsistence patterns or change. Thus, for instance, acorns were a staple food of the California Indians, who practised, in Harris' (1989) terms, wild-food procurement. However, acorns have also occupied a position of some importance in parts of Europe, Southwest Asia, and Japan practically until the present day, millennia after the introduction of agricultural systems - at the other extreme of the continuum, in plant-food producing systems. Their role as a potentially important food for both wild and domesticated animals adds a further dimension to the study of acorns, involving a still broader view of subsistence systems.

In order to examine the way that a study of acorns may contribute to a study of past subsistence, the archaeological record of acorns, and the ways it has been interpreted is first examined in this thesis. Ethnographic data on acorn use from as many regions as possible are presented, in order to provide both an idea of the potential variability of the roles of acorns in subsistence, as well as a background for ideas regarding the ways in which such variability might be related to the archaeological record. The present distribution of oaks is investigated, to give some indication of the extent to which there may be gaps in the ethnographic and archaeological information. Information on changes in oak distribution during the Late Pleistocene and Holocene, during much of which there is archaeological evidence of acorns, is also summarised. The ecology of oaks, especially relating to ways in which they might be affected by human disturbance, such as fire or the cutting of trees, is also examined.

Many models of past acorn use draw heavily on data relating to those biological characteristics which may affect the use of acorns as a dietary resource. Information on biological and ecological characteristics can be particularly useful, because it provides an

independent line of evidence with which to interpret the archaeological record. In theory this can act as a guard against the simplistic use of ethnographic or environmental analogy. This is particularly important in the study of acorns where most of the detailed ethnographic evidence comes from a few restricted areas, from which inferences might have to be made to areas where there is very little ethnographic data; or where a long timescale is involved. Particular attention is paid to the nutritional characteristics of acorns, and factors affecting them, including the presence of tannins, and other factors which may relate to their palatability, or their requirements for processing. These data are examined in detail, together with information on factors affecting the yields and availability of acorns to people, including both those factors affecting acorn production, including the masting habit, and those factors affecting acorn predation (much of which is presented in Appendices 3 and 4). A vast amount of information exists on many of these aspects, some of which is referred to within the literature on modelling the subsistence role of acorns. It was felt important to present these data in as full a form as possible, in order to determine the extent to which consistencies or variability can be detected within the resource, something which is necessarily often passed over in more concise accounts, and in most models of resource use.

The utility of the available biological data is examined, and the way in which such data has been used in modelling the past role of acorns is investigated. Finally, an attempt is made to bring together the evidence from all areas of study - archaeology, ethnography, and biology - and to examine the implications of this wide-ranging approach both for interpretations of the role of acorns in human subsistence, and for models of past human subsistence in general.

CHAPTER 2. ACORNS IN ARCHAEOLOGY

2.1. INTRODUCTION

Acorns are known from archaeological sites across most of the range of current oak distribution, from California in the western United States to Japan. In the Americas they are found also in sites from the Eastern Woodlands, and range from Mexico north to the Great Lakes. They are found across Europe and the Mediterranean in sites ranging in age from the Mesolithic until late Mediaeval times. They are known from Southwest Asia, from the Mediterranean coast as far east as Iraq. The major geographical gap in the archaeological record occurs from Iraq to the eastern seaboard of Asia.

There are both significant temporal and regional differences in the archaeological record, but, since most discussion of acorns tend to be regional in focus, the archaeological record is here reviewed in this way. The following does not constitute a full account of the acorn record in each area; instead, it is an attempt to illustrate the kind of evidence available in each area, and the kinds of interpretive approaches which have been adopted.

2.2. ACORNS IN ARCHAEOLOGY - A REGIONAL REVIEW

2.2.1. California

The study of archaeobotanical evidence of acorn use is relatively undeveloped in California and the west. Interpretations of the role of acorns in Californian subsistence have therefore relied heavily on inference from artefactual material and other physical evidence of processing technology, in strong contrast to the situation in eastern North America, to be discussed below.

2.2.1.1. Acorn finds and identification

Charred remains of acorns have been recovered from archaeological sites in California , but they are uncommon (Basgall 1987; Schulz and Johnson 1980; Schulz 1981), and finds like that described by Schulz and Johnson (1980), consisting of a "cache" of several hundred charred shelled acorns are rare. The paucity of acorn remains is perhaps not surprising, as archaeobotanical recovery of any kind has been relatively under-developed in the region, and has only recently begun to receive much attention. Basgall (1987) suggests that the poor record of acorns (and other plant remains) is due to the failure, especially of early excavators, to carry out systematic recovery; together with poor preservation, and - in the

case of acorns - the unlikelihood of them coming into contact with fire during the ethnographically most commonly-recorded processing treatments.

The paucity of remains means that it has rarely been possible to suggest the identity of acorns used in the past, other than by reference to those species available locally, and ethnographically-recorded "preferred" species. Whole acorns in the cache described by Schulz and Johnson (1980), were, however, identified as having greatest similarity to *Q. douglasii* and *Q. wislizenii*, neither of which was present in the immediate vicinity during historical times. Ethnographic work on the uses of bedrock mortars undertaken by McCarthy *et al.* (1985) has indicated that the internal dimensions of bedrock mortars may relate closely to characteristics of particular acorn species, particularly their degree of oiliness. There may be potential for inferring the use of particular species (or species with similar processing characteristics) from measurements of ancient mortars.

2.2.1.2. Other evidence for acorn use

The types of evidence used in discussions of the role of acorns in California archaeology have been summarised by Basgall (1987). His summary is based to a large extent on the work of Schulz (1981) who pointed out the problems with botanical and artefactual remains, and examined other evidence for subsistence change in relation to acorn use, in particular extending work begun by McHenry (1968) involving palaeopathological and demographic analyses indicative of changes in nutritional status and stress.

Artefacts for grinding or pounding, particularly mortars - either portable or as bedrock facilities - and pestles, are the principal source of evidence which has been used to infer acorn processing, and the dietary importance of acorns, in the past. The archaeologists' view of intensive acorn use has also been linked closely with the invention and use of basketry, particularly as a means of transporting large quantities, and as containers for cooking acorn mush (Baumhoff 1963; Heizer and Elsasser 1980). Other elements of technology traditionally interpreted as evidence of acorn use are the heated stones used in cooking mush, or substitutes of baked clay (Heizer and Elsasser 1980). The rock foundations of acorn granaries, which occur in places, though, like bedrock mortars, difficult to date, have been used as evidence of acorn storage (Jackson 1991). The unlikelihood of detecting ancient leaching pits has been pointed out by Basgall (1987), though Jackson (1991) notes that the frequent location of sites adjacent to dependable water supplies is consistent with the need for the large amounts of water needed for the leaching process. Soils high in ash and carbon are also interpreted as evidence of acorn cookery, and often occur in association with bedrock mortars (Jackson 1991).

2.2.1.3. Interpretations of artefactual evidence - technology

Much of the research into processing technology has focussed on the relative proportions of mortar and pestle and mano/metate (handstone/grinding slab), the first of which have traditionally been associated by archaeologists with acorn pounding, with the latter indicating the grinding of small seeds (see, e.g., Heizer and Elsasser 1980).

The predominance of the mano/metate in early sites has been used to infer an apparent change from an economy where small seeds were most important to one in which acorns came to predominate. Mortars and pestles in early sites were frequently small and ochre-stained, and were assumed to reflect uses other than acorn processing. Ethnographic work has demonstrated that the exclusive association of artefact type with particular plant food resources is unsupportable (Basgall 1987; Francisco 1976; McCarthy *et al.* 1985). There have been early finds of acorns in association with assemblages dominated by manos/metates (Basgall 1987; Schulz and Johnson 1980).

The potential for more detailed interpretations derived from analyses of processing facilities, particularly bedrock mortars, has been illustrated by work by McCarthy *et al.* (1985). Work with Western Mono people has demonstrated the very precise differences in function of mortar holes and pestles of different dimensions, and hints at their potential relationships with particular acorn species. They have also demonstrated that the use of counts of numbers of mortar holes and their relative depths, or apparent wear, cannot be securely related to length or intensity of occupation of sites, as has frequently been assumed by archaeologists (see also Francisco 1976; Jackson 1991).

The equivocal nature of the Californian artefactual evidence in detecting change in subsistence over time was drawn attention to by Schulz (1981, see also Basgall 1987). In particular, problems relating to differences in the site types (e.g., cemeteries vs. settlements) most frequently represented or excavated in early and later periods mean that true comparisons between predominance of grinding or pounding technology are difficult to make. The difficulty of dating bedrock mortar facilities has also been noted. Nevertheless, Californian archaeologists continue to consider the primary affinity of the mortar and pestle to be with acorns, and where they dominate in the archaeological record an intensive focus on acorns is inferred (Basgall 1987; Bouey 1987).

The possibility that relatively less detectable methods of processing , which did not involve the well-known shelling-grinding-leaching-cooking sequence, may have been utilised in the past has been given little consideration, though Gifford (1936) suggested that burial of

acorns in mud was a technique for tannin removal that probably pre-dated the more intensive method.

2.2.1.4. Models of acorn use

Early interpretations of the appearance and rise to dominance of the Californian "acorn economy" were related to arguments regarding the spread or independent invention of both the technology, and knowledge of techniques, required for complex processing (Driver 1953; Gifford 1936). Alternative approaches began in the early 1960's, with Baumhoff's (1963) seminal work, involving quantitative studies of the ecological relations between people and food resources.

Baumhoff attempted to model the relationship between Californian populations at the time of European contact, and the estimated yields of what he felt to be the three major resources in the state - acorns, game, and fish. All three were considered important not just because they were bulk staple foods, but also because of their potential storability, making them essential for surviving the lean period of the year. Though Baumhoff did not explicitly extend his model into the more distant past, he inferred an antiquity for intensive utilisation of acorns, including leaching, of at least 4 or 5000 years, based on finds of processing tools.

Baumhoff's demonstration of the abundance of resources, particularly acorns, and his suggestion that the acorn-based economy was capable of supporting higher population densities than would an agricultural economy, has been of particular influence in discussions surrounding the non-adoption of agriculture by California Indians, despite close contacts with Southwestern agriculturalists. It also produced a change in the way acorns were viewed, from a position which suggested that they were a resource which could only be exploited with recourse to complex processing, to one in which they were seen as a highly-valuable and nutritious resource. This implicit view has influenced studies of the nutritional and health status of prehistoric Californian populations, so that palaeopathological evidence indicating a change from poor status to an improved status has been linked with the adoption or intensification of acorn-eating (Basgall 1987; McHenry 1968; Schulz 1981)

Baumhoff's modelling did not consider in any detail the role of other plant foods. His interpretation of the presence of large numbers of processing tools - both manos and metates as well as mortars and pestles - in archaeological sites as evidence for acorn processing, was made partly on the basis that there were no other plant resources present in sufficient quantity to merit such an apparent reliance. Similarly, many subsequent attempts

to reconstruct the potential yield of food resources in California have very much focussed on acorns. Mayer (1976) estimated potential acorn yields to determine whether it was possible for ethnographically-recorded populations of Sierra Miwok Indians to have existed entirely on acorns, while Basgall (1987) estimated both potential nutritional yields of acorns and the energy costs of obtaining and processing them. An exception in the west is the work of Simms (1987), who carried out harvesting and processing experiments in the Great Basin to determine the relative returns per unit of time for various plant foods including small-seeded grasses, pine nuts and acorns. Reanalyses of Baumhoff's original work (Baumhoff 1981; Gage 1979) have elaborated his model, in particular to allow for the potential effects of competition for acorns by and with deer and other animals, and Gould (1975) developed a model similar to that of Baumhoff, incorporating plant and animal resources, as a "test" of adaptive responses among ethnographically-recorded northwestern Californians. However, the situation generally contrasts with that of eastern North America, where quantitative models (see 2.2.2.3.1.) have focussed on the relative costs and benefits of numerous resources, and where models have been explicitly related to archaeological data.

While noting that there were not comparable data available regarding other plant foods, Basgall (1987) emphasised the high cost of acorn processing, and the potential implications for the development of acorn economies. He suggested that need rather than availability had resulted in the concentration on acorns, and that the development of an economy apparently dominated by specialization on such a resource was indicative of prehistoric population growth and increased resource stress (see also Bouey 1987).

The existence of ethnographic data from which the demographic, settlement, social and political correlates of an acorn economy can be extracted, means that such have readily been associated with interpretations of past acorn use. Ziegler (1968), extending Spinden's (1917) and Heizer's (1958) suggestions, and finding support in Baumhoff's analyses, explicitly characterized Californian acorn economies as "quasi-agricultural", and discussed the influence of this economy on social structure. Many characteristics of acorn economies which are frequently associated with the development of agriculture elsewhere have also been discussed, and - by inference or directly - extrapolated into the past by Basgall (1987), Bouey (1987), and Mayer (1976). In particular the role of population stress as a reason for adoption of intensive acorn use has been emphasised, as has the role of storage and its effects on mobility, together with subsequent developments, including the elaboration of territoriality and exchange systems, and other social and political consequences. Jackson (1991) has discussed the introduction of the acorn economy particularly with regard to its social implications. He suggests that food procurement and production, seen in his model as controlled particularly by the decisions of women, and

specifically its focus on acorns, were "fundamental in structuring subsistence and settlement systems and other inter- and intra-community social and economic relations" (1991, 301), and that the development of such in the past can be examined via archaeological analysis of the development and distribution of bedrock mortar facilities.

2.2.1.5. Summary

Despite the poor nature of the archaeobotanical evidence, the role of acorns in the Californian past has been heavily emphasised, at times almost to the exclusion of discussion of other plant food resources. The emphasis on the importance of acorns and their associated technology, particularly in relation to the non-adoption of "agriculture', has been criticised by Bean and Lawton (1973), who draw attention to the great diversity of resources which were incorporated in the subsistence system, together with the modes of their extraction "some of which were semi-agricultural" (1973, xxxvi). Principal among these "semi-agricultural" practices was that of "Indian burning" whose beneficial effects on, amongst other things, the acorn crop and it s harvesting, has been given considerable attention by Californian anthropologists, and was reviewed by Lewis (1973). However, consideration of such alternatives and activities seems to have been rarely discussed in the archaeological literature of the region.

Because of the wide-ranging and detailed nature of the ethnographic data on acorn use and processing it has been heavily used, though there has been a tendency to extrapolate the data directly into the past, with little discussion of the possibility of temporal variability. The archaeological emphasis has therefore been on the transition to the acorn economy in the past, and changes in intensity or method of use over time have been little considered. It is only recently that the ethnographic record has been considered as having a more deductive role to play in the interpretation of the archaeology of acorn use. The approach being undertaken by workers such as McCarthy*et al.* (1985), discussed in 2.2.2.3, also illustrates the potential importance of detailed ethnographic work undertaken by archaeologists - many Californian ethnographies, while packed with potentially useful information, frequently lack the essential data which would make them more directly applicable to archaeological remains. Fortunately, in California, there are still people who gather and use acorns, and even if now preferring to use coffee grinders rather than mortars and pestles (see e.g., Duncan 1961), have considerable knowledge of the details of processing by previous methods, not to mention direct knowledge of factors such as those influencing the choice of particular species.

2.2.2. Eastern North America

There are strong contrasts between California and eastern North America in the approaches which have been adopted to the role of acorns in past subsistence. A far superior archaeobotanical record has meant that the emphasis has been on the direct interpretation of finds of acorn remains, and there is relatively little discussion relating to technology of the kind which dominates the Californian approach.

Eastern North America is one of the principal areas in which both the quantitative and ecosystemic approaches originally encouraged by the "New Archaeology" have been most enthusiastically applied. From the 1960's onwards there has been a considerable focus on subsistence, including the role of plants, and recovery and analysis of archaeobotanical remains has been given an importance which is seldom seen elsewhere. With the introduction of improved recovery techniques from the early 1970's onward, and the enormous increase in finds of plant remains, much of the the research focus has been on the "Eastern Agricultural Complex" and its native, small-seeded cultigens (see, e.g., Keegan 1987; Watson 1989). Nevertheless, there is still a considerable focus on the role of nuts as a subsistence resource, partly because nuts, together with wood charcoal, are frequently the most abundant plant remains found, and partly because there are considerable numbers of well-preserved early sites which largely pre-date finds of small-seeded cultigens, and where nuts are the principal food plant for which there is direct evidence.

2.2.2.1. Representation and identification

The majority of finds of acorns on eastern archaeological sites, like those of other nut genera, consist of small charred fragments of shell, often of maximum diameters smaller than 5mm, and probably most abundantly of even smaller dimensions (see 2.2.2.2.) (Gary Crites, personal communication; Lopinot 1982; see also Yarnell 1984). Fragments of acorn shell preserved by dessication have also been recovered, notably in the Salts and Mammoth caves of Kentucky, where they were also present in palaeofaeces (Yarnell 1969, 1974a, 1974b). There have also been finds of whole dessicated acorns in dry rockshelters (see, e.g., Hilliard 1980, 1981, 1986), and whole acorns in waterlogged sites (Kay 1986).

Some finds of acorn cotyledon are also recorded, though usually in much smaller frequencies or weights than acorn shell (e.g., Asch and Asch 1985b; Keene 1981b; Lopinot 1982; Munson *et al.* 1971), though in some instances cotyledon fragments may outweigh shell (e.g., Crawford 1982). Though only present occasionally, acorn cotyledon seems to be more commonly recorded than kernel fragments of other nuts. Finds of acorn

cupules are occasionally made, but these are uncommon (Gary Crites, personal communication, Hilliard 1980; Lopinot 1982).

Because of fragmentation it is rarely possible to identify acorns beyond the level of genus, since, for known criteria, the whole acorn, including cupule is necessary for identification to species level (and even then not all species can be separated). Finds of whole desiccated acorns in Ozark bluff-shelter sites have been identified by Hilliard (1980). Some, including acorns with cupules, were identified to species, though the majority were only identifiable as members of the red and white oak groups, separated on the presence or absence of tomentosity on the inside shell surfaces. However, it may be possible to make some useful inferences based on characters of charred fragments, and Lopinot (1982) commented that variations in shell thickness of acorns found in one site in the Illinois valley suggested exploitation of more than one species. Lopinot also attempted identification of acorn cotyledons, found both whole and as fragments, based on size characteristics and surface markings. In relation to known sizes of locally-occurring present-day species, he suggested that some belonged to small-fruited species, such as *Q. palustris*, *Q. stellata*, or *Q. falcata*, while others, including fragments ranging in length up to 15mm, were likely to have come from intermediate-sized species, though were probably not big enough to belong to large-fruited species such as *Q. macrocarpa* or *Q. rubra*.

2.2.2.2. Quantification

There has been a considerable emphasis on methods of quantifying archaeobotanical remains of all kinds on eastern sites, as exemplified by Hastorf and Popper (1988). Quantification by counts of numbers of individuals, as is normally used for seeds, is generally unsuited to fragmentary remains, and acorns and other eastern nuts are usually quantified by weight. Lopinot (1982, 1984) has pointed out the value of using weights and counts simultaneously, especially for correcting for bias against more fragmentary plant remains, such as acorn shell; and Asch and Asch (1985a) have suggested that the use of ubiquity (or frequency - a presence/absence measure of the percentage of samples in which a particular taxon is found), rather than absolute quantities (however measured) might enable more accurate characterisation of the importance of such resources as acorns whose remains were biased against.

In addition to problems of direct or relative quantification of plant remains, the problems involved in relating any quantified measures to the original subsistence base have been given some consideration. The lack of comparability between nuts, seeds, and other plant food resources as archaeobotanical remains is frequently pointed out (see, e.g., Lopinot 1982; Munson *et al.* 1971). Nuts have been noted to equate taphonomically, in some ways,

more with bones than with seeds, since the remains found in both cases represent discarded inedible portions, rather than edible portions as is the case with many seeds, and both are contrasted with fleshy plant parts such as fruits or tubers, of which edible portions may be preserved, but are less dense than either.

It is also generally acknowledged that within nuts, as a class of remains, there are problems of comparability relating to taphonomic differences, which need to be accounted for when attempting to reconstruct the subsistence pattern which the archaeobotanical record represents. Relatively early analyses of nut remains, such as those of Allison (1972), Asch *et al.* (1972) and Munson *et al.* (1971) discussed some of the problems of comparability. The need to take into account differing kernel-to-shell ratios, different shell densities, differential preservation and fragmentation, and biases which might be introduced by human factors, such as differences in processing techniques, were all acknowledged. In particular, the likely differences in all these respects between the thick-shelled nuts (hickories and walnuts especially), and the thin-shelled nuts (especially acorns), and the likelihood that such biases are partially responsible for the frequently high representation of thick-shelled nuts in comparison to acorns on many sites, were emphasised, as was the need for experimental approaches to this problem.

Some analyses have discussed the effects of, or attempted to make correction for, differences between genera in the shell-to-kernel ratio (e.g., Asch and Asch 1985a, 1985b; Lopinot 1982, 1984). Yarnell (1969, 1974b) used formulas of "food equivalence" to reconstruct the food intake represented by plant fragments, including acorns, in desiccated palaeofaeces, though these were apparently arrived at fairly arbitrarily. Generally though, there has been little attempt to investigate the other problems alluded to above, with the notable exception of the work of Lopinot (1982, 1984). Lopinot undertook a study of the taphonomic aspects of charring of different nut shells and kernels, together with the wood charcoal of these and other eastern trees. He measured the reduction in weight after charring of specimens, and their relative degrees of fragmentation, and calculated conversion factors which could be applied to weighed archaeobotanical remains. He also undertook measurements of the weight ratios of nut shell-to-kernel. Although he emphasised his work as only a preliminary study, certain conclusions could be made, including the greater weight loss and fragmentation on charring of acorn shells relative to others such as hickories and walnuts, as well as their considerably greater kernel-to-shell ratio. Though fewer analyses were undertaken on charring of kernels, it appeared that those high in fat, such as hazelnut, and by inference hickory and walnut, survived charring less well than did acorn cotyledon.

Lopinot emphasised the preliminary nature of his work, and it has unfortunately not been replicated or extended, despite the frequent discussions in the literature of potential biases in the nut remains. Many analyses continue to accept the archaeobotanical record more-or-less at face value, and, for example Asch and Asch (1986) suggested that it was unrealistic to expect to be able to correct for all the potential taphonomic biases that might be present in the archaeobotanical record, and consequently to produce direct estimates of the original quantities of nut foods, or any others, represented by their remains. Instead, they suggested, the most fruitful approach was to focus on changes in emphasis shown by different ratios of plant remains over time, or from place-to-place, an approach they felt was supported by some consistent temporal trends in analyses in the region under study. This type of approach, involving comparisons between samples and sites has been developed to a considerable extent in eastern North America, with increasingly sophisticated methods of relative quantification being undertaken (see summaries in Johannessen 1988; Miller 1988). Analysis of similarities and differences between samples in the ratios between nutshell and wood charcoal have been frequently made, and used as indicators of changes in the use of nuts (see, e.g., Johannessen 1984).

Such between-sample comparisons have many problems, especially when comparing sites on more than a relatively local basis. Although there is frequently standardised recovery and analysis between sites which are examined by an individual, or group of archaeobotanists, frequently working on relatively large-scale local projects, this standardisation does not always extend beyond such groups, and certainly may not be the same for earlier analyses. For example, taking three fairly recent groups of analyses, those undertaken at the Kampsville Archaeological Center, Illinois, sorted and quantified all material collected using mesh sizes of 0.6mm and above (Asch and Asch 1985a, 1985b, 1986); the Shellmound Archaeological Project, involving sites in Kentucky, used a smallest sieve-size of 1mm, but picked out only whole seeds below 2.38mm, and quantified the non-seed material between 1 and 2.38mm according to the ratios found in the >2.38mm fraction (Crawford 1982); and in the Saginaw Valley, Michigan, again, small seeds only were sorted from the <2mm fraction, but only counts and weights from the >2mm fraction were used in comparative analysis (Egan 1988). Any attempt to compare results between these areas could evidently be subject to biases introduced by variations in methods of analysis. In particular, comparable analyses of the smaller fractions, which are where the greatest differences between studies occur, may be of importance. Asch and Asch (1985a) have emphasised the far greater quantity of material, in terms of numbers of fragments, which occurs in the <2mm size fraction. Lopinot (1982, 1984) and Gary Crites (personal communication) have commented on the fact that acorn fragments are typically smaller than other nutshells (hickory, walnut or hazelnut) and that sorting of only samples above 2mm (or in some cases even larger) is likely to produce under-representation of acorns.

2.2.2.3. Interpretation and modelling

One of the earliest attempts at systematic interpretation of the archaeobotanical record was the "ethnobotanical" approach pioneered by Yarnell (1964) in relation to plant remains found in sites in the Great Lakes region. Data on plant remains found at sites in the region were listed, on a presence/absence basis. The paucity of plant remains other than nuts in Archaic sites was suggested to be largely due to problems of recovery and decay, rather than lack of utilization, but there was little further consideration of taphonomic bias, and all the nuts, including acorns, were placed together as taxa which might be expected to survive well. Summaries of local ethnobotanical records, for these, and other taxa, together with some of their biological and ecological characteristics, such as season of availability, were made. Yarnell suggested that inferences regarding both subsistence and season of occupation of sites could be made from analysis of the ethnobotanical record; and the implication of his work was that many of the gaps in the archaeological record could also be filled by this method. He also pointed out some of the drawbacks with such inferences, including the fact that, though there was an emphasis on wild rice and maple sugar in the ethnobotanical record, the importance of metal technology in the processing of the latter, and the importance of acorns as a famine food amongst the local agricultural populations, suggested that acorns may have been more important prehistorically.

Yarnell particularly emphasised the importance of the combination of biological and ecological studies with those of ethnobotany in attempts to interpret the archaeobotanical record and understand past human interactions. In particular he discussed the likely effects that human activities in the past (especially burning and deliberate or unintentional planting) may have had on plants, (drawing particularly on the work of Edgar Anderson, and his hypotheses such as "hybridization of the habitat" - see, e.g., Anderson 1948 - with its emphasis on the effects of human disturbance on the establishment of genetic variation in plants) and examined the potential role of modern studies of the distribution and genetics of plants, including trees, for detecting such past activities. Yarnell attempted an analysis of the relationship of hybridization to recorded plant use. Estimates of the extent of hybridity were compared for those families which had high usage recorded ethnobotanically. Only the Fagaceae, largely because of the high number of oak hybrids, and Corylaceae showed unusually high variation which he felt might be accounted for by heavy utilization (though other heavily-utilized families did not have unusually high numbers of hybrids).

Though the basic elements of Yarnell's "ethnobotanical" approach have been influential in eastern archaeobotany (though sometimes at its most basic this may consist of lists of plant finds accompanied by lists of the plant uses derived from local or regional ethnobotany, with little attempt to relate the archaeobotanical and ethnobotanical records in more detail),

the more detailed aspects of Yarnell's work have rarely been replicated, or investigated in more detail.

Another influential approach to archaeobotanical interpretation, which focusses on nuts, is that of Asch *et al.* (1972), at the Koster site in the Lower Illinois Valley. Although their analysis dealt largely with hickory nuts it is worth discussing in some detail as it drew attention (either explicitly or implicitly) to many problems regarding the interpretation of acorn finds (amongst other subsistence remains), many of which have not yet been resolved. The subsistence pattern at this site was interpreted against a background of what appeared to be great environmental stability, with a similar stability being found in the use of various nut species at the site over at least 3000 years of intermittent occupancy, largely because hickory nut fragments constituted over 90% by weight at all levels, with other nuts, in varying proportions, making up the remainder. Acorns, in the form of shell fragments, were present in very small quantities when measured by weight, but were the second most ubiquitous nut type, after hickory nuts, occurring in 51.5% of all samples. The authors used experimental data to produce an estimate of the total number of nuts represented by hickory nutshell finds on one level of the site, and of the number of trees of which this might represent a crop, but they did not make similar calculations for the other species' representability.

Asch *et al.* also compared the abundance of nut remains with those at the nearby Middle Woodland site of Macoupin, at which there was a significantly higher presence of small seeds. Acorns were somewhat less ubiquitous at this site, though percentage by weight in midden and feature samples was much the same as at Koster. While applying correction factors to account for taphonomic bias against seeds relative to dense nutshells, they did not attempt to apply any such factors to acorns, which are consequently classified as a minor food source at both sites, whereas seeds are seen to differ radically in importance between the two. However they did draw attention to the fact that acorn processing might be rather different from that of other nuts (and thus implicitly suggested that they might require different interpretation), as well as to the fact that acorns are nutritionally quite different from the other nuts, and therefore suggested that a change in the percentage of acorns over time would be especially significant as an indicator of a change in adaptation.

The frequent predominance of hickory nut in the archaeobotanical record has been related to use of bulk processing techniques, such as pulverising and boiling in water to separate nut shell from kernels and oil, and increases in their remains have been related to the introduction of such techniques, or improvements relating especially to the introduction of ceramics (Asch and Asch 1985a; Munson 1976 and Ozker 1977, both cited in Keene 1981b; Ozker 1982; Reidhead 1976; Styles *et al.* 1983, and, as explanation of finds of

hickory shell fragments in palaeofaeces, suggesting ingestion, Watson 1969). "Evidence" of processing of acorns is less frequent, though Lopinot (1982) comments on occasional finds of acorn cotyledons in pits similar to those which have been interpreted as leaching pits. The cotyledons were charred though, which does not suggest a process involving water. In some cases it has been suggested that the postulated differences in processing of hickory or other thick-shelled nuts in relation to acorns may be a partial explanation of the apparent differences in importance between the two groups seen in the archaeobotanical record. Apart from the purely physical differences which would assist their relative preservation, it is suggested that hickory nutshells may have had more opportunity to come in contact with fire, and consequently to be charred, as a result of the method of processing. Postulated techniques of acorn processing do not involve such proximity to fire, though Lopinot (1984) noted that parching of acorns, (to enhance storability or for other reasons) might increase the likelihood of finding their charred remains. Hilliard (1980, 1981, 1986) inferred from the semi-charred nature of desiccated whole acorns from rock-shelter sites that they had been parched or roasted prior to storing, probably to prevent destruction by weevils. The ease of removing shells of acorns, in comparison with those of hickory nuts, was suggested by Yarnell (1969) as part of the reason for the large quantity of hickory nut shell relative to acorn shell in human palaeofaeces from Salts Cave. It is also suggested that thick-shelled nuts are likely to have been a good fuel source, while acorn shells are less likely to have constituted a useful fuel (see, e.g., Keene 1981b; Lopinot 1982, 1984; Munson *et al.* 1971), though Lopinot has commented that the frequent absence of finds of charred nutshell from rock shelter sites, in environments where there would have been a high premium on fuel, suggests that nut shells generally were not used as fuel.

Lopinot (1984) has also examined the results of applying conversion factors derived from his experimental work described in 2.2.2.2, to interpretation of data from the Little Lower Tennessee Valley. A traditional interpretation, based on comparison of the relative weights of fragments showed dominance of hickory nuts, with some importance for walnuts in some periods, and acorns important only occasionally as secondary resources. The converted weights, however, which consisted of estimates of the original kernel weights represented by the archaeobotanical remains, showed acorns as the primary resource throughout, while hickory and walnuts were important, but only supplemental, resources.

One potential form of evidence for the use of acorns which is infrequently used in eastern North America is artefactual and technological evidence. One of the few studies of plant-based subsistence to have incorporated such material is that of Meltzer and Smith (1986). Stone and wood artefacts, including nutting stones, mano/metates and mortars and pestles were used, in combination with botanical remains, to infer intensive plant-processing, including that of acorns. The ethnobotanical record suggests the frequent use of wooden

mortars and pestles for processing acorns, and though Keene (1981b) commented that the almost complete absence of grinding tools in many of the sites he examined might imply the use of wooden mortars and pestles, the absence of wooden artefacts from most sites means that there has been little examination of the potential for inference of use or processing of acorns, or other nuts, from tools.

2.2.2.3.1. Optimising models of subsistence strategies

Throughout the eastern archaeobotanical literature the predominance of hickory nuts has generally been accepted as representative of the original subsistence strategy. Sites with small quantities of hickory and other nutshell may be explained by differences in site type or season of occupation (e.g., Asch and Asch 1986) or "local food preferences, aspects of seasonality and scheduling, or very local ecological situations", and perhaps by the change to plant cultivation (Crawford 1982, 213). Asch *et al.* (1972) explained the predominance of hickories at Koster largely as a result of their supposed nutritional superiority, in terms of quantity and quality of protein, and their fat content, which, they suggested, would be particularly beneficial to people subsisting on lean meat or fish; while the apparently small use of acorns reflected their assumed nutritional inferiority and higher processing costs. Such explanations, together with reference to the seasonal abundance of hickory, are often repeated (e.g., Johannessen 1984), with the first two of these qualities frequently contrasted with acorn characteristics. Because hickory nuts are frequently perceived as the most preferred food, instances where other nuts appear in increasing relative proportions have also been interpreted as indicating increasing pressure on resources, and the need to use less "preferred" foods (e.g., Lopinot 1982). The role of nut foods is thus assessed by what is basically a "least-cost" model (see Keene 1981b; Reidhead 1976 for discussion), in which selection of food is seen as an attempt to use potential resources optimally, in terms of obtaining maximum yield for minimum effort. The linear programming application of optimal foraging theory used by Reidhead (1976) to interpret sites in southeast Indiana, was proposed as an explicit test of the model of food selection used implicitly by Asch *et al.* The aim of this and subsequent similar models is to attempt to determine the hypothesised optimal solutions for satisfying nutritional (and sometimes other resource) demands at least cost, for a given population at a time and place often represented on an archaeological site or sites, and to compare these predictions with the subsistence pattern demonstrated by the biotic or other remains. This requires the estimation of hypothesised past population numbers and their dietary requirements, as well as the costs in obtaining and the nutritional gains in using various resources.

This Reidhead did for, amongst other things, nuts, requiring the use of biological, ecological, ethnographic and experimental data, to produce quantified estimates of yield

obtainable per hour of work. In the case of acorns and other nuts, yield characteristics were estimated from a combination of land survey reports on the numbers of trees of each species present, and an estimate of their annual yield derived from forestry and wildlife studies, together with the likely length of time of their availability. Allowances were made for losses to wildlife competitors, and for the proportion of the yield weight made up of nut shells. Estimates of the nutritional value of the predicted yield, in terms of calories, protein, and certain essential minerals and vitamins were made. Reidhead used a combination of data obtained from his own experiments and those undertaken by others (subsequently published as Petruso and Wickens 1984 and Talalay *et al.* 1984), based on ethnographic accounts, to estimate the time required for harvesting and processing activities. Though the many complex steps undergone mean that it is difficult to assess the reality of such estimates, one finding was that, contrary to Asch *et al.*'s assumption, when the requirements of procurement and processing were taken into account, the acorns of the red oak group (*Erythrobalanus*) (though not those of the white oak group) were in fact a better choice than hickory nuts, in terms of their returns for time input.

Keene (1981a, 1981b) used a model based on that of Reidhead to interpret Late Archaic sites in the Saginaw Valley, Michigan. The results suggested that nuts (including acorns, hickories, black walnuts, beechnuts and hazelnuts) would be of low value and would not be incorporated, on a systematic basis, in an optimal strategy. This was largely because of the high processing costs attributed to them, relative to animal foods, though the sensitivity to calcium requirements of the model also biased against nuts relative to animal foods. Modifications of the model assumptions enabled other predictions about nuts to be made, including the suggestion that, if there were limits on other foods, such as during a lean time of the year, stored nuts would be of much greater value. However, because nut-harvesting was assumed to occur at the same time as intensive deer-hunting - predicted by the model as low-cost and an optimal strategy - nuts were still predicted as unlikely to be harvested intensively.

Both Keene and Reidhead compared the results of their modelling with archaeological data. In neither case were attempts made to allow for taphonomic biases in the archaeobotanical record, though the likely effects of these were discussed. Keene, for instance, did not attempt to put any quantitative value on the finds because "current method and theory in ethnobotany does not permit us to assign quantitative significance to palaeoethnobotanical remains" (1981b, 183), and in particular he felt it was not possible to make inferences about the relative economic importance of plant foods in the diet based only on carbonised remains. He suggested that nut finds indicated only the local availability of those species, and little else. In Reidhead's case, the comparison was undertaken as a test of the hypothesis that optimization of diet had occurred at the site during the two periods under

examination. Conflict between the predictions and subsistence data suggested that optimal strategies were not always followed, and Reidhead suggested that factors other than work effort and biology must be involved in human choice of foods, though some differences were also explained as due to weaknesses in the model. Keene discussed many of the difficulties inherent in the "testing" of models, concluding that this was not a valid use of them, because conflict or congruence between models and data could be equally ascribed to practical problems, such as inadequacy of the archaeological database and inability to interpret it, as to correctness or otherwise of the model. He suggested instead that the major utility of the exercise was in forcing the modeller to consider "which distortions are products of site-formation and which distortions are products of the model-building process" (1981b, 226).

Another modification of Reidhead's data and model, which considered Archaic subsistence adaptations through the midwest oak-hickory forest as a whole, was that of Christenson (1986). In contrast to Keene's model Christenson simplified the nutritional inputs to the system, so that he considers only energy, and predicts that hickory nuts and red oak acorns would together be the most important plant foods (his approach again draws on the work of Reidhead and therefore suggests similar processing costs for these resources), and would increase in importance through the Archaic as a postulated population increase caused a relative increase in the cost of procurement of foods like deer, while encouraging a greater use of resources whose use could be intensified without increasing the relative costs of finding them. His model was compared with the archaeobotanical and archaeozoological record from carefully-selected sites - those with systematic recovery and flotation programmes - throughout the Midwest, including the Koster site. Christenson noted the very low quantities by weight of acorn shell at all the sites, and, even after using the conversion factors developed by Lopinot (see 2.2.2.2.) to transform nutshell weights for all genera to their equivalent calories found that acorns still did not reach the predicted quantities. Early and Middle Archaic values were closer to those predicted by the model than were those of the Late Archaic, when they showed an "inexplicable decline". Christenson discussed other possible taphonomic differences between acorns and other nuts, relating especially to different methods of processing, but did not consider in detail how, or whether, these might have had some bearing on the results.

Lovis' (1986) work involved a re-examination of the archaeological record discussed by Keene, and drew attention to the disparity between Keene's model predictions of non-use of nuts and the fact that their remains were nevertheless present at all the sites considered. He noted especially that by other criteria none of the sites is thought to have been occupied in the autumn, and that the presence of nut remains is therefore more signicant as it implies storage. Based on evidence for heavy nut utilisation in the Late Archaic of the Weber site,

on the upland margin, close to where the majority of nut trees would be likely to occur, Lovis suggested that there may also have been a bias against nuts in the archaeological record, because of the concentration of sites examined by Keene in the lowlands surrounding the former Shiawassee Bay. He accepted Keene's predicted position for acorns and other nuts as being generally poor-choice foods, even at the upland margin, and suggested that the inhabitants of the Weber site may have been forced to follow a less-than-optimal strategy, and include nuts in their diet because of the likelihood of periodic failure (due to flooding) of the more optimal lowland habitat. He also compared the frequency of nut remains with that of wood charcoal of nut-producing genera, and suggested that it was possible to detect selection of nuts in ratios which did not relate to the ratios of these genera collected as firewood, and that this might even reflect conservation of nut trees.

Egan (1988) also compared nut shell and wood charcoal at the Weber site, and suggested that though low frequencies of acorn remains in the Middle Archaic of the same Michigan site could be accounted for by burning of forest floor material or rodent caches, frequencies in the Late Archaic, especially if corrected for taphonomic bias, together with the association in samples of acorn remains with those of other nuts, implied that they may have been an important part of the subsistence strategy. She noted that, as wood charcoal of the white oak group, with acorns requiring less elaborate processing, was dominant in the site, the archaeobotanical data were consistent with an ethnographic record which she suggests shows a preference for sweet acorns. Though the Weber site was interpeted as being only a temporary camp during the Middle Archaic, and the limited nature of the data on this period in the area is contrasted with the more intensive site occupation and larger available database on the Late Archaic, the potential effect of this on the archaeobotanical record does not seem to have been considered, and the increase in nut finds in the later period was interpreted as evidence for the development of intensive nut harvesting.

In eastern North America the presence of wood charcoal has frequently been used to infer the local presence or abundance of particular tree species, and comparisons between the wood and nut remains of the same species have been used in interpreting the importance of the nuts. Munson *et al.* (1971), for example, compared the relative abundances in samples at the Middle Woodland site of Scovill of several thick-shelled nuts with the predicted yields of these species based on local vegetation and productivity studies, and found the proportions to be similar. They suggested that there was no selection of nuts of particular species, other than for those which were most locally abundant. However, acorns were present in samples in much smaller proportions than they would be if they related directly to yields, even when the bitter red oak acorns were excluded from estimates. Munson *et al.* concluded that even if corrections were made to allow for differences in shell-to-kernel ratios, and differences in preservation these would be unlikely to account for all the

discrepancies between predicted yields and acorn shell remains, if acorns had been collected at the same rate as the other nuts. Ozker (1982) at the Schultz site, again in the Saginaw Valley, suggested selection for hickory, butternut and walnut relative to acorns based on the relative proportions of nutshell remains to wood charcoal of the relevant genera.

2.2.2.3.2. Vegetation reconstructions

Though vegetation reconstructions are frequently utilised in archaeobotanical and archaeological reports simply as an environmental backdrop, many of the studies discussed above draw attention to the importance of local environmental reconstruction when attempting to interpret the archaeological record. Accurate vegetation reconstruction is essential if estimates of past yields of acorn or other resources are to be made. The use of land surveys as analogies for past vegetation is frequent, and Reidhead's use of them in reconstructing nut tree yields has already been mentioned. Other examples include those of King (1976a, 1976b), and Zawacki and Hausfater (1969). Many of the problems with both use of land survey data, and such reconstruction attempts in general, have been discussed by Green (1984), Lopinot (1984), Petruso and Wickens (1984), and Reidhead (1984), and the estimates of Zawacki and Hausfater reassessed.

Despite Yarnell's early discussion of the influence of past human activity on vegetation (see above, 2.2.2.3.), there has generally been little discussion of the effect that such activities could have, either on vegetation reconstruction, or on archaeobotanical or archaeological interpretations. In particular, though land surveys often represent vegetation which has not been directly modified by recent Americans, and thus were considered representative of "pristine" vegetation, they were undertaken at a time, in the east, when native populations had been very much reduced for a considerable time, and the potential consequences of this need to be accounted for. Asch and Asch (1985a, 1985b, 1986), for instance, have commented on the extensive ethnohistoric evidence for burning of the forest, and the effect that this may have had on both distribution and yields of oaks and other nut-bearing trees, and noted that "the natural environment can no longer be regarded as simply an independent variable in the study of human adaptation" (1985b, 341).

The importance of understanding environmental variability and fluctuations in resources at various scales has been emphasised by some archaeobotanical interpretations. The presence or absence of nutshell, including acorns, has in many cases been interpreted in relation to site seasonality, with presence usually indicating autumn or winter occupation, and, in combination with remains of other foods, available, for example, in spring or summer to suggest storage (e.g., Munson *et al.* 1971; Styles *et al.* 1983; Yarnell 1969).

On a slightly longer time-scale, Asch *et al.* (1972) drew attention to the possible influence of mast cycles, in nut trees in general, but particularly acorns, on their reliability as a resource. It was noted that "it will be particularly important to determine if the masts of single species are regionally synchronised or whether single trees or groups of trees have mast cycles which are essentially randomized. It will also be necessary to discover if the masts of several species tend to be synchronized or whether they complement each other..... results could suggest whether in poor years nuts could be obtained by going farther afield, by turning to other nut species, or even abandoning one area for another where the masts were better" (p. 25). Asch *et al.* also comment (p.10) that "if mast cycles of different species are not synchronised there should be variability from one year to the next in nut proportions [in archaeological samples]."

In Egan's (1988) study at the Weber site, mentioned above, spatial separation between walnut and acorn shells at the Weber site were inferred to provide evidence for variability in production of mast of species from year to year. Examination of several sites of the same period in the locality showed no apparent predominance of any one nut species, and it was suggested that this indicated either use of whichever species was abundant in any one year, or exploitation of a wide variety of species in any one year. This finding was related to the less productive and reliable nature of resources at this latitude, in comparison with midwestern sites, resulting in an opportunistic subsistence adaptation during the Late Archaic.

This discussion has illustrated the fact that much of the interpretation of archaeological finds of eastern North American acorns has been undertaken in terms of their use relative to other resources. However, not all acorns are necessarily equivalent resources. In particular, as some of the discussion of models relating to nutritional qualities have indicated, there is a difference between acorns of the red and white oak groups. As noted in 2.2.2.1. these cannot easily be distinguished as charred archaeobotanical remains. In the case of finds of caches of partly-charred whole desiccated acorns from several bluff shelters in the Ozarks Hilliard (1980, 1981, 1986) was able to differentiate the acorns into the two groups. Acorns of the red oak group appeared to predominate, and Hilliard discussed possible reasons for this apparent preference by the Mississippian occupants, relating to productivity, likely numbers of different species in the area, differences in storability, and nutritional differences. Unfortunately, his approach is probably only possible at the moment with exceptionally well-preserved acorn finds, but it does indicate the potential of some of the kinds of inferences which could be made about past use based on variations in the acorn resource.

2.2.2.4. Summary

Though there has been a considerable focus on the use of nut resources in prehistoric eastern North America, nuts are often lumped together for discussion, and where there is seperate discussion the role of acorns is frequently discussed less than that of others, especially hickory nuts. Emphasis in the area has been very much on direct analysis of food remains, and in contrast to California, discussion of, and inferences from, artefacts or other non-biotic evidence are relatively infrequent. Despite the fact that work by Lopinot has suggested that acorn remains on archaeological sites could be greatly under-represented relative to other nuts, the focus has remained on those genera which are more readily apparent. The failure by all but a few to attempt to allow for even those biases which are undeniably at least partially quantifiable means that resources such as acorns continue to be biased against in analysis, and often do not receive the attention in interpretation that they might, in some cases, deserve. At many sites the emphasis on interpretation is very much on the addition of, or transition to, a subsistence strategy in which small seeds played a more important part, and the increasing focus on this aspect of archaeobotany may partially explain the lack of attention given to analysis of nuts in general, and acorns in particular. In addition, the local ethnohistoric and ethnographic record strongly emphasises the role and elaborate processing of hickory nuts in particular, and references to acorn use are fewer (though, interestingly, probably not as sparse as references to use of small seeds).

2.2.3. Mexico and Central America

Despite the fact that Mexico is the centre of the greatest diversity of oak species in the world there has been relatively little consideration of the possible role of acorns in past subsistence there, or elsewhere in Central America.

2.2.3.1. Evidence for acorn use

Most acorns recovered have been in the form of desiccated remains, from dry cave sites. Very small numbers were recovered from the Coxcatlan cave in the Tehuacan Valley (dated to 5000-3500B.C.) and the Palo Blanco site (dated 200B.C. - 700A.D.) (Byers 1967). Though detailed analyses of human coprolites were also undertaken, no evidence of acorns was recorded (Callen 1967). A charred acorn cotyledon, together with domesticated plants, was recovered from the Middle Formative period site of Fabrica San Jose (Ford 1976).

Large quantities of acorns, preserved by desiccation have been recovered from Guilá Naquitz, Oaxaca (Smith 1986). Most acorns seem to have been whole, and in their shells, some with cupules. In some levels oak leaves were also present, but no attempt seems to

have been made to identify the species concerned (though the caption to an illustration (Smith 1986, fig. 19.5) indicates that at least two species are shown).

Grinding stones, including mortars, pestles, manos and metates, occur at a relatively early date in many Mesoamerican sites. Bainbridge (1985b) has inferred the processing of acorns from the presence of large numbers of grinders and mortars from the Tehuacan Valley 1500 years before maize is thought to have become important. At Guilá Naquitz a variety of mortars, manos, and metates in levels dated to 9000-7000 B.C. were suggested, by association with plant remains in the same level, to have been used for grinding or pounding of acorns, as well as piñon nuts, mesquite, and other large seeds (Flannery 1986). Despite the expected association (presumably by analogy with California) of mortars with acorn processing, Flannery notes that mortars increase in levels where acorns decrease, relative to mesquite.

2.2.3.2. Analyses and interpretations of acorn use

Bainbridge (1985b) has commented that the presence of only few, or no, acorn remains in Mexican sites should not necessarily be interpreted as an indication that they did not contribute to subsistence. He suggested that acorn processing would leave little in the form of plant remains, and that storage in granaries similar to those in California would leave little archaeological trace. However, the major reason for the small representation of acorn remains in archaeological sites has probably been the failure to attempt systematic recovery of plant remains on many sites, together with the focus of much study by Mesoamerican archaeologists on urban sites, and on topics other than that of subsistence. When subsistence has been considered the major interest has been with the development of agriculture, and the focus by archaeobotanists has been very much on the evidence for, and processes leading to, the domestication of maize, beans and squash, and to a lesser extent other species; and the role of wild plant foods has been given relatively little consideration. Finds of acorns at the Coxcatlan and Palo Blanco sites on the Tehuácan Valley were listed in the non-food uses section of the plant remains report by Smith (1967). Sanders *et al.* (1979, 288) state that "a number of [the genera indicated in the pollen sequence from Zohapilco] .... e.g., *Quercus* ....are probably not food resources"; though Ford (1976) suggests that acorns may have been collected and stored at Fabrica San Jose at a time when there was apparently an increasing focus on domesticates.

The dominance of acorns in the archaeobotanical record at Guilá Naquitz has meant that there has been considerable discussion of their role in the subsistence of the inhabitants (Flannery 1986). Much of Flannery's interpretation of subsistence was undertaken by modelling the local environment and foods represented at the site, elaborating the systemic

approach first used by MacNeish in the Tehuácan Valley (see Byers 1967). The environmental setting of Guilá Naquitz suggested a paucity of food resources through much of the year, and, together with the season of availability of most recovered plant foods, has led to its interpretation as a seasonally-occupied site, from August at the earliest, to spring. Acorns were apparently a major autumnal resource.

Storage of acorns in pits appears to have occurred occasionally, while most of the acorns, apparently abandoned by the inhabitants in large numbers at the end of occupation phases, were "stored" in large piles on the cave floor. Spatial distributions of the acorns, and their occasional association with pits and ground-stones were used to infer such storage and processing areas, and in combination with other data, reconstructions of intra-site spatial organisation were made, related by Flannery to men's and women's activity areas.

Flannery also discussed some of the potential taphonomic biases affecting the archaeobotanical data, including the problems of comparing different foods, especially those whose remains are represented by inedible, versus edible, portions. The relatively poor representation of foods which can be eaten unprocessed, and therefore are more likely to be consumed outside, was contrasted with that likely for foods, especially acorns, which "cannot be eaten raw...[and]...had to be brought back to the cave after harvesting" (1986, 252). Acorns were likely to be over-represented in the archaeobotanical record, relative to some other foods. However no attempt was made to allow for any such taphonomic biases when quantifying and modelling plant food resources since "almost certainly the errors we would introduce would be as great as any already inherent in the data. The raw figures from the cave, however imperfect, at least reflect the activities of the prehistoric occupants, rather than the fantasies of the archaeologist" (1986, 253).

Following the method used in the Tehuácan valley where acorns were not included in the modelling process, direct extrapolation of the quantities of food represented by the acorns and other plant foods were made for each occupation level. Nutritional analyses of the major food resources were undertaken, and reconstructions of the varying contributions to nutritional requirements of the postulated population made. Carbohydrate was present in low proportions in many of the foods, and acorns were postulated to have been by far the largest provider, while fats were considered to be rather low in the plant diet. Environmental reconstructions of the local area were also made based on macrobotanical and microfaunal remains, and pollen analysis, and including a relatively long-term study (over seven years) of the yields of food plants and their fluctuations, especially with regard to unusually dry and wet years.

Incorporation of these estimated data enabled predictions to be made regarding the area utilised by the prehistoric populations. The data were also incorporated in a computer-generated decision-making model (Reynolds 1986) which compared the reconstructed foraging subsistence system with one into which "incipient agriculture" was incorporated. Though most of the discussion of the model focusses on the "incipient domesticates" themselves, there was some discussion of predicted consequences of incipient agriculture for other resources. One prediction was an increase in focus on acorns, as the modelled group spent more time gathering near the cave, though Reynolds comments that this prediction was not supported by the archaeobotanical record, in which acorns showed a slight decrease over time.

2.2.3.3. Summary

A relatively poor archaeobotanical record, and an emphasis on the development of agriculture, means that along with other wild food resources acorns have been largely ignored in discussions of subsistence in Middle America. Even the ecosystemic approaches of MacNeish and Flannery, though dealing with sites in which wild plant remains are abundant, have had an explicit focus on the question of the adoption of cultigens. The work undertaken at Guilá Naquitz indicates the potential importance that acorns may have had in the diet of Middle Americans, and the presence of acorn finds in periods in which domesticates have been incorporated in subsistence strategies indicates, together with the ethnohistoric record (see 3.2.3.), that they may have had an importance in places where agriculture was apparently the predominant subsistence mode. However, such hypotheses have yet to be examined in any detail in the region.

2.2.4. Europe and the Mediterranean

2.2.4.1. Evidence for acorn use

Acorns have been recorded as charred or waterlogged remains from many European sites, covering all periods from the Mesolithic to the Mediaeval (see, e.g., Bahn 1984; Bradley 1978; Gasco 1983; Guilaine 1976; Jacomet *et al.* 1991; Jørgensen 1977; Marinval 1991; Renfrew 1973; Vencl 1985; Wasylikowa 1984). Vencl (1985) has compiled many archaeobotanical records of acorns, covering Europe and Southwest Asia, and records their presence in "storage pits", sometimes with other food plants, as well as in various storage receptacles; and in other contexts such as graves, in association with quernstones or hearths, or in one case in bowls in an oven. Acorns are almost always found as single or joined cotyledons, sometimes with shells. Fragmentary remains, of shell or cotyledon, are

rarely recorded, except in close association with finds of whole acorns or cotyledons (e.g., Buurman 1990; Jones and Rowley-Conwy 1984).

The role of processing technology in providing evidence for acorn use has been little addressed. In later sites they are almost invariably inferred to be associated with cereal-processing (though see Dolukhanov 1979), while during the Mesolithic, as Zvelebil (in press) notes, although pounding stones and other ground-stone technology are widely reported from European sites they are rarely interpreted as plant-processing tools. The one major exception to this is in work taking place in Corsica and Sardinia, where a very recent ethnographic record of acorn use exists. Here, grinding and pounding implements, including "cupules" in the bedrock, are common, as are finds of large quantities of charred acorns in some sites. Ceramic artefacts similar to those recorded ethnographically are found, including perforated vessels interpreted as acorn-flour processors, and flat plates similar to those on which acorn bread was made. In combination, these finds have been suggested to provide strong evidence for extrapolation of the ethnographic record as far back as the Chalcolithic (see Lewthwaite 1982, 1989 for summaries).

Identification of acorns to species has rarely been addressed, though Buurman (1990) and Jørgensen (1977) in northern Europe mention the problems in separating *Q. robur* from *Q. petraea* on acorn characteristics alone, while Lewthwaite (1982) notes that acorns specifically identified as *Q. ilex* have been identified on Corsica and Sardinia.

2.2.4.2. Interpretation

One problem with interpretation of acorn remains as a human food resource encountered in Europe - at least on some sites - which does not generally arise in other parts of the world, is the possibility that they were gathered for domestic animal food. Jørgensen (1977), suggested that it was unlikely that finds of charred acorns represented acorns gathered for animal consumption, since the animals could more easily be sent into the forest to forage for them. This view, and the interpretation - of charred remains at least - as evidence of their use as human food, has generally been accepted (see, e.g., de Ceunynck 1991; Pals 1984; Vencl 1985).

Of the 103 European and Southwest Asian sites listed by Vencl (1985) as containing acorn remains only two were from non-agricultural sites. Though Vencl himself stresses the incomplete nature of the data summarised, acorn finds are relatively rare on Mesolithic sites (see, e.g., Zvelebil in press). However, with the exception of the ubiquitous hazelnut, this is the case for all plant remains. Although plant remains are interpreted as food when recovered, their role during this period has in most cases been dismissed as unimportant,

primarily due to their low abundance relative to animal bones. Price (1987, 288), summarizing the data on the Mesolithic in western Europe concludes that "plants other than hazelnut provided only a minor contribution to the diet". Both Lewthwaite (1982) and Vencl (1985) have suggested that the absence of acorn remains in Mesolithic sites, relative to their greater representation in later periods, implies that their use cannot represent any continuation of Mesolithic wild-plant use, but that acorns should be seen explicitly as part of the Neolithic (and later) economy.

From the Neolithic to the Mediaeval, where sizeable quantities of acorns have been found, they have been inferred to have been an important gathered element of the diet (see e.g., Buurman 1986; de Ceunynck 1991; Dolukhanov 1979; Gasco *et al.* 1983; Jørgensen 1977; Kroll 1984; Pals 1984; Vencl 1985) with their potential role as a supplementary or famine food during times of failure of agricultural crops often emphasised (see, e.g., Jørgensen 1977; Kroll 1984; Lewthwaite 1982; Lundström-Baudais 1984). Jørgensen (1977) suggested that they may also have been a normal element of the subsistence strategy in parts of Jutland which were marginal for agriculture. Kroll (1984) and Lundström-Baudais (1984) have inferred from an absence of acorns that the agricultural economy of the period concerned was succesful enough not to require the inhabitants to resort to all available sources of food, and Kroll also relates increases in acorn finds towards the end of the Early Bronze Age at Kastanas to the collapse of the local farming economy and culture. Lewthwaite (1982) notes correlations of increasing finds of acorns with periods of political and economic strife throughout the region.

Acorn remains on archaeological sites in Europe are rarely considered in terms of any of the aspects of their processing or taphonomy which might affect their relative representation, either over time or between different sites, and consequently might aid in interpretation, though Vencl (1985) notes that processing by grinding and boiling is likely to result in lower archaeological visibility than roasting. Jørgensen (1977) contrasted the find of acorns recovered from the Neolithic site of Vorbasse in South Jutland, consisting solely of charred kernels with no evidence of shells, with the form in which hazelnuts occur on this and other sites - as shell fragments. She suggested that differences in processing requirements between the two nuts was a likely explanation - hazelnuts could be consumed immediately (with their shells presumably thrown on the fire), while acorns would need to first be processed in bulk, with the shells removed prior to this (though the question of why the large quantity of acorn shells would not also be disposed of similarly was not addressed). Jørgensen suggested that the acorn kernels themselves were being processed by roasting or boiling, and had been accidentally charred. Similar interpretations have been made by Pals (1984) of a find of charred acorn cotyledons from the Neolithic site of Aartswoud, and by de Ceunynck (1991) of charred germinating acorns. Buurman (1990), discussing a sample

of 25 litres of charred acorns recovered from Iron Age pits also suggests that the find represents the discarded remains of an unsuccessful roasting process. In this case shells were present, though they had fragmented during or after the charring process. Curiously, in the European literature finds of charred acorns are often referred to as "roasted", and with few exceptions, such as those listed above, more circumspect interpretations are not made regarding the precise means by which acorns became charred.

2.2.4.3. Models of acorn use

The emphasis of most archaeobotanical research in Europe has overwhelmingly been on post-Mesolithic sites, and on domesticated plants (see, for example, the three most recent reviews of the subject - Renfrew 1991; van Zeist and Casparie 1984; van Zeist *et al* 1991). In combination with the rather empirical, inductive approach which has tended to dominate European archaeobotany, this means that there have been few attempts to model the potential role of acorns in their relation to the rest of the subsistence system.

Such modelling approaches have been much more heavily utilised in relation to Mesolithic subsistence. However, partly because of the paucity of plant remains recovered from European Mesolithic sites, consideration of plant use has rarely been emphasised in these models. Clarke (1976) attempted to redress the balance in favour of plants by pointing out the taphonomic, as well as cultural, biases that have partly contributed to the greater representation, and consideration of the role, of animal resources during the period, and drew attention to the potential for exploitation of plant food resources in the region. Subsequent discussion of Mesolithic plant use has frequently been dominated by reference to Clarke's model, but there has been little attempt to develop or extend it, either theoretically or methodologically, though Zvelebil (in press) has recently suggested some of the directions into which investigation could be extended.

Probably the major modelling trend dealing with subsistence which has developed in Europe is the "palaeoeconomy" approach of the Cambridge school, frequently using site-catchment analysis (see, e.g., Higgs 1972; Higgs 1975; Jarman *et al.* 1982), and its various offshoots. However, as is the case with much of the Mesolithic research which involves itself with the examination of subsistence, the major focus has been on transitions to agriculture. Despite the explicit recognition of taphonomic bias aginst the representation of plant foods, their subsistence potential is rarely discussed in detail, and animal resources have been almost exclusively focussed on in the Mesolithic itself, while in transitional and later periods plant resources are often only considered indirectly or directly in terms of potential grazing or arable land. There has consequently been little emphasis on the role of any wild plants.

Some attempts to apply quantitative approaches very similar to the cost-benefit models used in Eastern North America have been used in modelling subsistence, often by Americans working in the region, and often deriving much of the quantitative biological and environmental data, together with ethnographic analogies, more-or-less directly from North American studies. Price (1978), while suggesting that plants may have played an important role in Mesolithic subsistence, noted the lack of archaeological evidence for this, and they were assigned an arbitrary value of 15% of the diet in his predictive model. Plants were assumed to be primarily available in summer, with nuts used in autumn, and no plants were included in the model over winter. Though he suggested that hazelnuts might have been stored, and that there was some support for this proposition in the archaeological record, he excluded the effects of such storage from the model. While mentioning the possibility that acorns, among other plants, may have been utilised, Jochim (1976), interpreting Mesolithic sites from the Alpine foreland of southern Germany, excluded plants from the modelling process. Gregg (1988) has used a similar approach to Early Neolithic sites in the same area. Acorns were not recovered from any of the sites under consideration, and she therefore excluded them from her discussion, except with regard to their potential as food for pigs. However, Gregg does include hazelnuts in the modelling process, using quantitative estimates of hazel productivity modified from those made by Keene (1981b) in Michigan.

One quantitative approach to interpretation of European Mesolithic sites of the Ertebølle culture using some European productivity data, and giving more consideration to the potential role of plant foods, was that of Rowley-Conwy (1984a), who used a combination of his own data on collection rates for various resources, and that collected by Perlman (1980) in Eastern North America. The estimated return rates for acorns and hazelnuts were among the highest for locally-available resources. However, the focus of Rowley-Conwy's study was on the role of shellfish, particularly oysters, in the diet; and their value, in providing the major food during the winter and spring, was especially emphasised in his model for the transition to agriculture. Consequently any potential implications of the plant food returns were not investigated further, though Rowley-Conwy did suggest that storage of hazelnuts (and presumably, by implication, acorns) would have been difficult in the conditions of the Ertebølle.

Strangely, despite the strength of palaeoenvironmental studies in many parts of the European area, there have been few attempts to integrate such studies fully with subsistence modelling, though the future potential for such an integrated approach has recently been emphasised (Kvamme and Jochim 1989; Zvelebil in press). Lewthwaite (1982) related palynological evidence for the spread of evergeen oaks in the Mediterranean, to the archaeobotanical and artefactual evidence, and noted increasing evidence for acorn use as

the dominance of evergreen oaks increased. Morais Arnaud (1989), discussing subsistence data from shell-midden sites in the Sado Valley of Portugal, used analogies with modern vegetation to suggest that *Q. suber* was likely to have been the most common species in the area during the Mesolithic. As acorns of this species are relatively bitter, in relation to *Q. ilex*, which he inferred would have been more common inland, he suggests as likely that they would have required roasting or parching, and that this would have increased their chance of being found charred. Despite acknowledging the fact that excavations were undertaken in the 1950's and 1960's, and that plant recovery was unlikely to have been ideal, Morais Arnaud therefore suggested that their apparent absence from excavations could be interpreted either as a result of the absence from, or scarcity of oaks in, the area, or as due to neglect of the resource. He concluded that plants certainly made only a small contribution to the diet.

2.2.4.4. Summary

Because nearly all considerations of subsistence in Europe, from the Neolithic (and sometimes earlier) onwards, have been biased towards analysis of domesticated plants and animals and agricultural products, wild plant foods have often merely been recorded as present on archaeological sites, with little consideration given to their potential importance. Where acorns are found they are usually characterised as a famine food, based partially on the evidence of a rather undetailed ethnographic record. There has been little serious discussion of the processing requirement of acorns, or attempt to relate this to either archaeobotanical or artefactual remains, and other than basic comparisons with such plant remains as hazelnut shell, there has been little consideration of the role of taphonomic processes, or of the implications this could have for fuller interpretation of finds of acorns. Despite wide quotation of David Clarke's (1976) model of Mesolithic plant use, and the increasing emphasis on the use of wild plants in "agricultural economies" (Greig 1991; Moffet *et al.* 1989; see also Dolukhanov 1979; Jørgensen 1977), the potential role of acorns in either of these contexts has yet to be fully addressed in the European/Mediterranean region.

2.2.5. Southwest Asia

2.2.5.1. Evidence

Acorns are recorded from sites largely in the present or former oak-forested part of Southwest Asia. They occur principally in charred form, though desiccated acorns have also been recovered, including some identified as *Q. ithaburensis* ssp. *macrolepis* from

Nahal Hemar cave (Kislev 1988), and an acorn impression in clay has been recorded at Beidha (Helbaek 1966).

As with the European Mesolithic, plant recovery from the Epi-Palaeolithic has so far been rather poor. Charred acorns have however been found at the Late Palaeolithic site of Ohalo II (Kislev *et al.* in press), dating to 19,000 B.P. In the later village and urban sites, however, acorns, together with other wild food plants, often occur together with finds of domesticated cereals and other agriculturally-produced foods - e.g., at Çatal Hüyük, where some were found next to a hearth "as if about to be roasted" (Helbaek 1964), and Çayönü in Turkey; at Jarmo in Iraqi Kurdistan; at Arad in the northern Negev, etc (see van Zeist *et al.* 1984; also Dolukhanov 1979 and Zohary and Hopf 1988, for summaries).

2.2.5.2. Artefacts, processing technology, and other indirect evidence for acorn use

In the frequent absence or paucity of plant remains, especially from early sites, much discussion has surrounded the artefactual evidence for plant utilisation and processing. Byrd (1989) has summarized the debate surrounding such inferences. He notes that while, as in California, mortars and pestles have traditionally been assumed to provide evidence of nut-processing, while querns and handstones have been inferred to suggest processing of cereal grains, the improbability of such an exclusive association has been more recently questioned (see also Wright 1991). Goring-Morris (1987) has suggested, based on the change from mortars and pestles to quernstones, that cereals were a relatively late addition to a nut-based diet which predominated in the Natufian of the Negev. Byrd also noted the replacement of mortars and pestles by querns and handstones in the Levant during the early Neolithic, and suggested that this may represent technological improvement related to an increasing reliance on domesticated cereals, and does not necessarily imply a change in the type of plant resource processed. Wright (1991) has also noted the problems introduced to any such analyses by the numerous conflicting definitions and typologies which have been used for such tools throughout the area.

Perhaps because of the intensity of the debate, few specific inferences regarding the relationship between the artefactual evidence and specific nut resources have been made, though Bohrer (1972) and subsequently Bainbridge (1985b) have both presented models of acorn use in Southwest Asia incorporating inferences from artefactual evidence, and Stol (1979) has combined linguistic data with artefactual evidence to infer intensive processing of *Pistacia terebinthus* in the Jebel Sinjar of northern Iraq. Solecki (1969) has also suggested that acorn-processing may have been a major use of the abundant querns, handstones, and quern-mortars of the early village site of Zawi Chemi Shanidar, in the Zagros mountains in northern Iraq. There is recent ethnographic evidence of acorn-use in

this region, and it may be that the absence, or poor documentation, of such evidence elsewhere in Southwest Asia has militated against such inferences.

One further type of processing technology present in Southwest Asia is bedrock mortars (see, e.g., Wright 1991; Younker 1989). Younker noted wide distribution across the region of "cupmarks" or "cupholes", and listed many previous interpretations of them, few of which involved plant-processing, and none of which included use as acorn-grinders. By analogy with similar features recorded ethnographically as acorn-pounders in California and the Zagros Mountains in western Iran, he suggested this as a likely use. Again by analogy with Californian data, he listed various characteristics of archaeological sites that might be used to identify potential acorn-processing locations. They would be expected to occur in areas of past woodland, would have surface bedrock outcroppings complete with cupmarks, and would be near sources of water for leaching the ground meal. He identified several sites which fulfilled the required parameters, including Tell el-'Umeiri in Jordan; as well as numerous sites within the Mt. Carmel area in Israel. Many of these were caves, which he suggested would be ideal for storage of acorns. Unfortunately acorn remains themselves had not been recovered from any of these sites.

2.2.5.3. Interpretation and modelling

There has been considerable emphasis on subsistence adaptations in Southwest Asia, especially in the period leading up to the domestication of crop plants. Approaches involving environmental reconstruction were pioneered in the region (Braidwood and Howe 1960), and the concept of the "broad-spectrum revolution", of which acorns were suggested to have formed one component, and which has been so widely applied in other parts of the world, was first developed here (Flannery 1969). However, as Byrd (1989) notes, there have been relatively few attempts in Southwest Asia to model the availability of food resources. Those that do exist have been concentrated in Mesopotamia, probably beyond the limit of oak vegetation. Possibly a major factor in this, at least with regard to the modelling of plant food resources, is that, despite the theoretical emphasis on the available "broad spectrum" of resources, the archaeobotanical focus (if not necessarily the archaeological one), has been, as in Europe, on the domesticated cereals and legumes and their wild relatives, and to a lesser extent on other domesticated fruit and nut species (see, e.g., Miller 1991). This focus on cereals, as (Byrd 1989, 172) has commented "has strongly affected the direction of research and interpretive models of Natufian subsistence", and a similar conclusion could be reached regarding other periods here, and throughout the region as a whole.

Interestingly, Helbaek, who was the first archaeobotanist to systematically examine plant remains in this area, appears to be one of the few to have attempted any kind of systemic interpretation, suggesting that nuts such as acorns, almonds, pistachio and hazelnuts, would have been the major provider of fats in the area, with carbohydrates coming from the grasses, and protein from animals (Helbaek 1970). Unfortunately subsequent archaeobotanists have not developed Helbaek's approach, and Byrd has emphasised the need for research on "the potential density, expected yields from individual plants or trees, nutritional yields, and amount of energy involved in collection and subsequent preparation of wild legumes, fruits, and nuts" and suggested that "undoubtedly there exists interspecies variability in edibility (for acorns due primarily to the amount of tannin), yields, and predictability of good yields" (1989, 172).

One attempt to use quantitative modelling of some aspects of food resources in the region is that of Russell (1988), who utilised a cost-benefit approach to model the beginnings of food production. He compared estimates of wild einkorn collecting and processing with similar estimates, including those for acorns and pine nuts, collected by Simms (1987) in the Great Basin of North America. His conclusion that the returns from wild einkorn would be greater than those from other potential food sources, including acorns, have been criticised, partially on the basis that the technology used was a poor analogue for traditional technology. When using more appropriate techniques, the processing costs of cereals would be considerably greater than Russell's estimates, while other resources, including tubers, fruits and other nuts, as well as acorns, could be processed by less intensive methods and would provide better returns (Wright 1991).

Given the poor archaeobotanical evidence, combined with the absence of detailed biological and ecological data, much of the modelling regarding the potential use of acorns in the region has been rather hypothetical, and has drawn heavily on ethnographic analogues, often from California. Many of these discussions have focussed largely on the changing role of acorns with the adoption of domesticated plants.

Bohrer (1972) hypothesised an initial situation in which wild cereals and legumes were first utilised as animal fodder, together with tree leaves, principally of oaks, while people focussed on acorns as their major food source. However, as the animal populations increased as a consequence of human assistance, the oak forests were gradually degraded by overgrazing. With the reduction in browse, seeds of wild annuals were broadcast to increase the food supply for animals, resulting eventually in domestication, and their adoption as the major source of human food as the acorn harvest also diminished. Bainbridge (1985b) has hypothesised a similar process, with the addition of the need for fuel-wood, and changes in climate both leading to reductions in acorn supply.

Many of the components of such hypothesised "acorn economies" are seen as pre-adaptive for the subsequent use of cereals, following implicitly Flannery's (1969) characterisation of grinding technology and storage facilities as pre-adaptive. The idea of the pre-adaptative nature of storage facilities has been further developed by Testart (1981, 1982) with special reference to acorn storage, for which he used ethnographic analogies from California. A primary role for acorns in the origins of agriculture in Southwest Asia has also been suggested by Rosenberg (1990), who suggests an early focus on acorns as a principal resource in an area stretching from the Levant, through the Taurus and Zagros mountains. Rosenberg uses an ethnographic analogy from the Great Basin, where focus, including ownership, on pinyon pine as a principal food resource occurred, while processes intended to increase productivity of resources were focussed on the more easily-manipulated small-seeded annuals. He infers a similar possibility in Southwest Asia, with population pressure leading first to ownership of oaks, with associated increases in territoriality and sedentism, and, when the consequent need to intensify resources arose, leading to the application of manipulatory practices to the wild progenitors of the domesticated cereals. These practices eventually lead to their cultivation, and then their elevation to a position as primary plant food resource. In Rosenberg's model storage only becomes important as the "produced" food source gains in importance.

Few discussions involving consideration of acorns as a potential food source have dealt with periods later than the period prior, or the transition, to "agriculture", despite the occurrence of acorns in sites of later periods. One exception is that of Younker (1989). While suggesting that acorns may have been a normal element of the subsistence strategy in pre- and early-agricultural sites he suggests that, because of the time-consuming leaching process, they would only have been resorted to later in times of great need or political instability. He notes that the site of Gezer, inferred from artefactual and locational evidence (see 2.2.5.2) dates to the Early/Middle Bronze age when local urban life was apparently in decline - many sites of this age in the valleys were apparently abandoned at this time, while those in the hills were being utilised. He relates the decline of urban sites to failure of the agricultural system, and suggests that at such times an alternative hunter-gatherer or herder-gatherer lifestyle would be adopted, with people forced to fall back on alternative food sources, such as acorns. Younker also commented on the fact that most local excavation in the later periods has focussed on urban sites, presenting problems in testing his theory, and suggested that more intensive investigation of non-urban camps and settlements might provide more evidence of such a revertance to subsistence strategies based on wild animal and plant foods.

2.2.6. Eastern Asia, including Japan

2.2.6.1. Introduction

A problem with any discussion of archaeological investigations in this part of the world is the disparity between the enormous amount of excavation and associated study which is taking place, especially in Japan, and its accessibility to the non-Japanese (or Korean, etc.) reader. In this summary, therefore, I am following the practice adopted by others of dealing largely with the "western-language" archaeology while acknowledging that this approach must inevitably be incomplete (cf. Barnes 1990; Rowley-Conwy 1984b).

There are few detailed archaeobotanical reports from this region. This partly reflects the extent of archaeobotanical investigations, which have yet to make significant inroads into the archaeology of China, or what was the Soviet Far East. Even in Korea, Hudson (1990) has recently noted the paucity of archaeobotanical data. Acorns have, however, been recorded here, though from only seven sites, ranging in age from the Neolithic to the Proto-Three Kingdom period (1st Millenium A.D.) (H. Watanabe 1990, cited in An 1991. These areas have largely, therefore, been excluded from western-language discussions of non-agricultural subsistence. Zvelebil (1986) while explicitly attempting a comprehensive review of the Mesolithic of temperate Eurasia, and giving coverage of Central Asia and western Siberia, was unable to include any areas further east, except Japan. Bainbridge (1985b) has noted that parts of China were forested by oaks in Mesolithic times and would be well worth investigating with acorn-use in mind. At the moment, however, it is difficult to say anything about acorn use in these areas, and the following discussion is confined to Japan.

2.2.6.2. Evidence for acorn use

One particular problem with general discussions of subsistence, or subsistence remains, in this area is the difficulty of ascertaining precisely what is meant by "acorn", both by Japanese archaeologists and westerners. Apart from its application to nuts of the genus *Quercus*, the word is used for those of both *Castanopsis* and *Lithocarpus* (see Kidder 1968, 1973; Koyama 1978; Nishida 1983; Pearson and Pearson 1978).

Though there has been some emphasis on studies of past subsistence, and subsistence modelling, in Japan this has unfortunately not coincided with detailed archaeobotanical, or even - though to a lesser extent - archaeozoological studies (Hudson 1990; Ikawa-Smith 1980; Rowley-Conwy 1984b). However, nut remains have often been recovered and identified, especially from Jomon sites. Nut remains recovered from Jomon sites were

summarised by Sakazume (1961, cited in Kidder 1968), M. Watanabe (1969, cited in Pearson and Pearson 1978, 1975, cited in Ikawa-Smith 1980), and more recently by Koyama (1978). Acorns identified to species include *Q. dentata*, *Q. acuta*, *Q. serrata*, *Q. acutissima*, *Q. mongolica* var. *grosseserrata*, *Q. glauca*, and *Q. gilva*, and other nuts include species of *Castanea*, *Castanopsis*, *Lithocarpus*, *Aesculus*, *Juglans*, *Torreya* and *Gingko*. Many of these finds come from waterlogged sites, which probably explains the frequency of finds of nuts of *Castanea* and *Aesculus*, which have been infrequently recorded in other parts of the world. Most nuts are apparently whole, and in the case of acorns, presumably in some cases include cupules, enabling such specific identification, though details regarding identification are unfortunately absent from western-language treatments. Acorn shell fragments are also recorded (see Kidder 1973).

Because of the recent, and often still-continuing use of all kinds of wild, and sometimes cultivated, nuts, including both acorns and "buckeyes" (the relatively toxic nuts of *Aesculus*), finds of their remains are readily accepted as evidence of their use as human food. Discussing the waterlogged plant remains from the early Jomon Torihama site, which included acorns of *Q. acuta* and *Q. serrata*, together with other nuts of*Juglans*, *Castanea*, and *Lithocarpus* Yasuda (1978) inferred that many of these were gathered by the inhabitants on the basis that their predominance as macro-remains was proportionately greater than their values as pollen. Although "carbon fragments" are mentioned, he did not discuss charred food-plant remains. The implications of the charring of plant remains for the evidence they may provide in relation to human usage generally seem to be unacknowledged, perhaps because so many sites contain plant remains preserved by waterlogging. Nishida (1983, 316), in a discussion largely based around nuts and other plant foods, commented that certain sites "provide few remains of food resources except carbonized seeds" and that reconstruction of the subsistence economy had therefore to rely on other evidence. Investigations at the Hamanasuno and other sites in southwest Hokkaido in the 1970's constituted the first attempt at systematic recovery of plant remains involving flotation, and Ikawa-Smith contrasted the 37 plant taxa recorded from 208 Jomon sites listed by M. Watanabe (1975, cited in Ikawa-Smith 1980) with the 180 taxa from five sites recovered by Crawford with the use of flotation (see Crawford *et al.* 1976; Crawford 1983). Ikawa-Smith notes that, though nuts are the most frequently-recorded plant remains from Jomon sites, this is probably because they are more likely to be recovered using "traditional archaeological methods" - hand-picking of readily-visible remains (see also Koyama 1978). Generally, a rather uncritical attitude to the archaeobotanical evidence seems to be prevalent in the western-language literature. Kato (1987) suggested that the "mode of subsistence [of the Jomon people] has been known since before the war", and "it has long been known that the basis of Jomon subsistence consisted of nut varieties such as chestnuts, walnuts, and acorns" (1987, 29).

Artefactual remains, principally grinding or nut-cracking stones, and other archaeological data have been used to infer evidence of acorn processing, often based on recent ethnographic data from the area (see Aikens and Higuchi 1982; Akazawa 1986a, 1986b; Akazawa and Maeyama 1986; Ikawa-Smith 1980, 1986; Koyama 1978; Kidder 1973; M. Watanabe 1975 cited in Ikawa-Smith 1980). In some cases pottery vessels have been found containing acorn remains, and some types of pottery have been inferred, by ethnographic analogy, to provide evidence of storage of starch extracted from various root and nut resources - see Chard (1974), Ikawa-Smith (1980), Kidder (1968). However, there is generally little discussion of the implications of contextual or other archaeological evidence either for human usage such as processing, or in relation to taphonomic processes.

Though many recorded finds of acorns and other nuts are from the Jomon, this may be partly due to the long time-period covered, and, in the western-language literature, due to an emphasis in interest on this period. Acorns are certainly found on later sites, e.g., in sites of the Kofun period (A.D. 300-600) (Chard 1974). However, discussions of subsistence from the Yayoi (which follows the Jomon) onwards have focussed almost exclusively on rice, and although there is discussion of other domesticated plants, there is apparently little consideration of the role of wild plants (Hudson 1990). Since the discovery of remains of plants which were subsequently cultivated at the early Jomon site of Torihama in the early 1960's (see Kato 1987; Yasuda 1978), much of the focus of discussion even of this period has centred on the extent to which Jomon people were cultivating other, sometimes indigenous, plants prior to the appearance of rice. Most attempts at interpretations of the role of acorns and other nuts in past subsistence have therefore focussed on the Jomon period.

2.2.6.3. Interpretations and modelling of acorn use

The modelling approach to past subsistence has been frequently used in Japan. Perhaps because of the relatively undeveloped nature of archaeobotanical investigations most of the modelling approaches have been heavily biased towards environmental or ecological reconstructions, with ethnographic analogues, especially for the Jomon period, sometimes drawn from Japan's still-surviving hunter-gatherers, the Ainu, now present only on the northern island of Hokkaido. Unfortunately, oaks and many other nut -bearing trees are more-or-less absent from this area, and there is consequently little ethnographic data available. The major exponent of Ainu ethnographic studies has been H. Watanabe, who has suggested that plant foods, including acorns were not important resources during the Jomon, based partly on analogy with the Ainu, together with ethnographic observations of alternative uses for grinding and pounding technology (H. Watanabe 1986). Ethnographic analogues for nut use tend to be based on more recent studies of use of such resources

derived from written records and recent studies of practices continuing until recent times in rural areas, particularly mountain villages. Though there is little western-language quantitative data available, deciduous oaks (largely those of sub-genus *Quercus*) are said to be more productive than evergreen oaks (largely sub-genus *Cyclobalanopsis*), while evergreen oak acorns are sweeter than those of deciduous oaks.

There are two major foci to discussions of the role of nuts in the Jomon. One concerns the extent to which nut trees were manipulated to improve their resource potential; the other concerns the reasons for the differences between western and eastern Japan during the Jomon, and in particular the relationship such differences may have had to the eventual acceptance of rice-based agriculture.

The debate surrounding "agriculture" in the Jomon, began before the recovery of remains of small-seeded cultigens, with Sakazume's (1957, cited in Kidder 1968) suggestion that the abundant remains of chestnuts and acorns on archaeological sites implied their cultivation or manipulation, and that sedentary sites had grown up near nut-bearing trees. The history of arguments surrounding the extent to which the plant-basis of Jomon subsistence consisted of gathered wild plants, including especially nuts of various kinds; or involved the manipulation, tending or planting of nut trees; or included a large component of cultivation of small-seeded annuals, have been discussed at length in the western-language literature, and summarised by Chard (1974), Crawford *et al.* (1976), Ikawa-Smith (1980), Kidder (1968, 1973), Pearson and Pearson (1978), and Rowley-Conwy (1984b). They depend to a large extent on arguments as to what constitutes "agriculture" (especially whether nuts can be considered as agricultural products), as well as the extent to which high-density, ceramic-using, possibly sedentary, populations and complex material culture could be supported without plant cultivation.

With the rather poor evidence provided by archaeobotanical remains, arguments have drawn heavily on inference from other archaeological and artefactual evidence. In support of the possibility that Jomon subsistence could have been based largely on the gathering of plants, especially nuts, from the wild, comparisons have been drawn with Californian "acorn economies" (Chard 1974), and local ethnoecological data on the productivity and reliability of wild resources, including acorns (Fujimori 1960, cited in Kidder 1968) have also been used. As Kaner (1990) suggests one of the more important results of this debate is the great interest which it stimulated in investigations of subsistence, often based on ecological approaches, and "set in terms of productivity, seasonality, carrying capacity and the relationship between social organisation and ecology" (1990, 38).

However, perhaps because the nut resources are so diverse in Japan, and because there is apparent evidence for exploitation of all of these, few discussions have focussed explicitly on acorns. One fairly recent attempt to develop Sakazume's hypothesis of nut-tree cultivation, and to relate it more closely to both archaeological and ecological data, was made by Nishida (1983). Quantitative estimates of different resources in the diet were extrapolated from plant and animal remains at the Torihama site. The weight of various remains were converted to estimates of the weight of edible parts, and then to their relative caloric inputs to the diet, and the broad nature of the subsistence economy, including gathering of plant resources, hunting, and fishing, was emphasised. Walnuts and chestnuts did not apparently make a great contribution to the diet, in contrast to the evidence from highland villages, where fewer subsistence remains were recovered (althoughx chestnuts and walnuts were relatively common), and where artefactual evidence was largely used to reconstruct the diet. The situation was related to a model based on ethnographic and ecological studies of a modern village, where the increases in sun-loving plants, including chestnuts and walnuts, in disturbed habitats around villages were characterised as "cultivation", in contrast to gathering which involved products from undisturbed primary forest, including "acorns" of *Castanopsis* and *Quercus*.

As noted above many of the modelling approaches have focussed especially on regional variability within Jomon subsistence strategies. Yasuda (1978) used detailed palynological studies in an attempt to relate changes in vegetation to cultural changes, including changes in subsistence. For instance, the change in dominance from deciduous oaks to the less productive evergreen oaks in the southwest of Japan, which occurred during the Jomon, was related to the beginnings of cultivation, resulting eventually in the adoption of rice-based agriculture, as the reduction in wild resources could no longer support the high population which had grown up in the more productive deciduous forest. Yasuda also related the later spread of the rice-based agricultural Yayoi culture to the northward advance of the evergreen forests.

Akazawa (1986a, 1986b; Akazawa and Maeyama 1986) concluded that at least until the later part of the Jomon, subsistence was primarily based on hunting and gathering, with some cultivated plants possibly used towards the end of the period; and he similarly focussed on regional variability within Jomon subsistence strategies, and its possible impilications for the slower acceptance of rice as a major agricultural staple in the east than in the west. Based largely on a statistical analysis of artefacts, he concluded that western Jomon subsistence was more heavily focussed on rather generalised plant-procurement, while in the east there was more specialized technology and a system based around a complex seasonal round involving consecutive specialisation on a number of resources. Plant resources provided the stable primary food source throughout Japan. Acorn and other

nut productivity was seen as particularly important, and stability in supply was provided by storage, for which there was evidence from the presence of remains in storage pits. However, in the east, this reliance on plant resources was supplemented by highly productive marine resources, exploited in spring and summer, which supported a large population with a high density of settlement. Rice was more rapidly accepted in the west partly because of lower marine productivity, with the pre-adaptation of the plant-processing technology for rice processing also important. In the west the major focus of subsistence activity would have occurred in autumn, with gathering of acorns and other nuts having little potential scheduling conflict with rice-growing, whereas the spring and summer fishing activities in the east would conflict with the planting and tending of rice.

Akazawa's suggestion that plant productivity throughout Japan was fairly similar contrasts somewhat with the estimates made by Koyama (1978, see also 1981), who examined the productivity of various resources throughout the Jomon period, and attempted to relate these to estimates of Jomon population, based largely on site numbers. The higher productivity of the eastern mixed evergreen and deciduous forest, with high population density, was contrasted with the lower productivity of the evergreen forests of the west, with low population density. Estimates of resources were made based on modern density in modern environmental analogues, and characterisation of resource yields as poor, moderate, or abundant. Koyama felt that any attempt at greater precision would be misleading. Though there was little precise data on acorn yields (in comparison to nut trees such as chestnuts and buckeyes which have had an important economic value in more recent times) a fairly stable supply of acorns was assumed, from the fact that oaks are the principal component of the Japanese forest. Koyama noted as well the general correlation between site numbers and oak-pollen abundance during the Jomon. The association of Jomon sites with highly productive mountainous areas was contrasted with that of later agricultural sites which were clustered in the less productive (largely in terms of wild-plant resources) lowlands, suited to wet-rice agriculture. Koyama also examined the archaeobotanical record for the Jomon period, and concluded that technological developments in plant processing could be detected over time. Walnuts, which required no processing, were the commonest nut on early sites, with evergreen oak acorns appearing relatively early. The more bitter deciduous oak acorns, which require more leaching, do not appear in the archaeobotanical record until the middle of the Jomon, and the nuts of *Aesculus*, which require the most intensive processing before they are edible are the latest to appear. Koyama also commented that later Jomon sites tend to be situated near springs and suggested that this was probably due to the need for water to leach acorns and buckeyes. This latter suggestion contrasted with that of M. Watanabe (1975, cited in Ikawa-Smith 1980), who examined the techniques and artefacts used for intensive processing of deciduous acorns and buckeye, still remembered in mountain villages, and

compared these with artefacts recovered from sites, suggesting that such technology was available in the early part of the Jomon.

2.2.6.4. Summary

Despite the poor quality of most archaeobotanical data, nut remains, including acorns, are one of the more commonly recovered plant remains in Japan. Modelling of plant-food resources, based on detailed ecological and ethnographic data, has been developed to a considerable degree in Japan. There is, however, no real consensus regarding the relative importance of acorns, other nuts, or other plant foods, and differences may depend to a certain extent upon the contrast between the two most commonly-used ethnographic models - that of the northern Ainu, amongst whom nuts, and plant foods in general, were apparently not of great importance, and that of recent rural, mainly mountain villages, where acorn and other gathered plant resources have continued to be of great importance until recently. Little detailed archaeobotanical analysis has been undertaken, and little attention has apparently been paid to taphonomic factors which may have affected the formation of the archaeobotanical record. The relatively poor quantity and quality of the archaeobotanical data means that it is difficult to assess the validity of some of the conclusions reached in models regarding acorn or other plant use.

CHAPTER 3. THE ETHNOGRAPHIC RECORD

3.1. INTRODUCTION

The use of acorns as human food is well known and extensively recorded. The use of numerous species has been reported, and records cover much of the area over which *Quercus* is distributed. Several general ethnobotanical compilations provide extensive lists of those species recorded to have been used, on either a regional or world-wide basis (see e.g., Bainbridge 1985a; Hedrick 1972; Howes 1948, 1974; Mabberley 1987; Menninger 1977; Morris 1927; Smith 1929; Tanaka 1976; Uphof 1968; Yanovsky 1936). The intention here is not to attempt to provide a comprehensive list of species used, but to present information on the way acorns have been used historically in different areas, and to attempt to give some indication of the roles they have had in subsistence. The available information varies widely in quality and degree of detail. Undoubtedly the most extensive and detailed record of the use of acorns as human food comes from California, but there are also reasonably good accounts of some aspects of use in Japan, the eastern United States, Europe, especially the Mediterranean region, and Southwest Asia. Some information, but with very little detail, comes from mainland eastern Asia and from Central America. Acorns have also played an important indirect part in human subsistence, through their role as major food for both wild and domesticated animals (see Appendix 4). The role of acorns as food for domestic animals in traditional subsistence systems is widely documented in Europe, and to a lesser extent Southwest Asia.

3.2. THE ETHNOGRAPHIC RECORD

3.2.1. California and western North America

3.2.1.1. Introduction

The first documented record of the use of acorns by native Californians is that made during Cabrillo's expedition of 1542; but acorns were still important in the late nineteenth and early twentieth centuries when ethnographers most intensively studied the region. Acorns are still commonly eaten, especially at festive occasions, by Californian Indians who have fully adopted western lifestyles and eating habits (see e.g., Eargle 1986).

3.2.1.2. Acorns in the subsistence system

Several workers have attempted to estimate the importance of acorns in native Californian diet. Steven Powers (cited in Heizer and Elsasser 1980) estimated in 1877 that the Indian diet consisted of 56% acorns (with 28% fish and 14% small seeds). Driver (1953) considered acorns to have been a true staple, being eaten in greater quantity than any other plant or animal genus. Kroeber (1953, cited in Balls 1962) estimated that acorn soup or mush was the chief daily food of more than three-quarters of the people, and, according to Barrett and Gifford (1933) the Miwok considered the acorn to be the finest vegetable food. Barrows noted that the oak was not as common in Cahuilla territory as in other parts of California and considered the acorn as "not of great economic importance" (1900, 62), but Bean and Saubel disagreed with this conclusion and pointed out that despite the relatively low density of oak trees the acorn was "unquestionably the most significant food source among the Cahuilla" (1972, 123). The fact that the acorn was so important despite the fact that oak trees were not particularly abundant here emphasises its value. Oaks could be up to 20 miles from main village sites, but oak groves were visited annually. Some workers have questioned the over-emphasis on the "acorn economy" in the ethnographic and archaeological literature (see e.g., Bean and Lawton 1973). Heizer and Elsasser (1980) have emphasised that the California Indians had a generalised subsistence strategy and used a diversity of foods, enabling them to fall back on others should any particular resources fail. Nevertheless, acorns were undoubtedly a major plant-food resource, (though not necessarily the only one), throughout aboriginal California.

In parts of western North America outside California oak trees become rather scarcer, so that in the Great Basin, Arizona and New Mexico foods such as the nuts of several pine species, mesquite, and/or cultivated maize apparently took on the role of principal plant food, e.g., amongst the Paiute and Shoshone (Steward 1933, 1938), the Navajo (Downs 1972; Elmore 1944; Vestal 1952) and Apache (Opler 1941). Most of these groups did use acorns as well, sometimes trading for them (see e.g., Steward 1933), but they were not apparently such a dominant element in the diet. The Southeastern Yavapai of central Arizona, for whom mescal, various cacti, and mesquite were probably the principal food, considered acorns a delicacy for which they would travel far, though they only ate the sweet acorns and not the bitter species also found in their locality (Gifford 1932b).

Acorns are a principal food of many North American animals (see Appendix 4), and must have played an important indirect role in human diet in this way. Apart from being eaten indirectly, in the form of hunted meat, acorns played a useful role in the hunting itself. Many animals were attracted to oak groves when the acorns were ripe, and hunting was particularly good. Acorn-gathering was usually accompanied by the hunting of quail, deer

and small rodents, all attracted by the abundant acorns (Bean 1972; Bean and Saubel 1972; Kniffen 1939).

There appears to have been considerable ownership of oak groves and/or individual oak trees in California. Among the Cahuilla, groves were owned by lineages, and individual trees were owned by families (Bean and Saubel 1972); trees might belong to individuals amongst the Wintu (Goldschmidt 1951); amongst the River Patwin acorn lands were free to all members of the tribelet, though seed-gathering tracts were individually-owned, while the Hill Patwin had rights to patches of oaks, though acorns were then shared within a settlement (Kroeber 1932); among the Tolowa, acorn tracts were private and inherited (Drucker 1937); amongst the Pomo ownership could be by individuals, families, or whole settlements (Loeb 1926; Kniffen 1939); the Wappo had oak trees jointly-owned by groups of relatives (Driver 1936).

Acorns are also one of the most frequently recorded trade items in the region - in the south, e.g., the Kamia traded watermelons which they had grown, for acorns collected by the Diegueno (Heizer and Elsasser 1980), the latter also trading "prepared" acorns with the Yuma and Cocopa (Castetter and Bell 1951); there was trade between plain- and mountain-dwelling Miwok for species of acorn found only in one or other environment (Barrett and Gifford 1933); the Nisenan traded for favoured species (Beals 1931); between desert-dwelling and other Cahuilla, the latter obtaining pinon nuts, mesquite and palm tree fruits in exchange for acorn meal (Bean and Saubel 1972); the Patwin sometimes sold shelled acorns (Kroeber 1932); the Owens Valley Paiute, on the edge of the Great Basin, traded pine nuts for acorns (Steward 1933); the Pomo would travel to trade for acorns if they began to run short over winter (Kniffen 1939); the Shasta sometimes traded pine nuts for acorns (Dixon 1907).

The social importance of various activities surrounding the actual processing of acorns have also been emphasised by California anthropologists, especially the shelling of acorns, and their pounding at bedrock mortars, and they were one of the most important foods at social gatherings and festivities (see, e.g., Bean and Saubel 1972; Goldschmidt 1951; Jackson 1991).

3.2.1.3. The harvesting/processing sequence

3.2.1.3.1. Harvesting

The acorn harvest was a prominent point in the seasonal round. It was often marked by the movement of many members of a village (as much as half to two-thirds - Bean 1972), and

travel to a camp in the oak groves would occur either en masse or in family groups (Gould 1975). Such camps would be occupied for perhaps 3-4 weeks, and could be more than a day's travel from the main (winter) camp (Bean and Saubel 1972). The Pomo would travel high into the mountains for the favoured tanoak acorns, though other species abounded nearby (Kniffen 1939).

The practice of picking or knocking acorns from the trees before they fell seems to have been most common thoughout California, though Barrett and Gifford (1933) noted that the Miwok of central California waited for acorn-fall before harvesting, and Waugh (1987) cites one report of the harvesting of both acorns knocked from the trees in September, and others subsequently picked up from the ground in November (see also Spier 1978). Opler (1941) notes that the Apache, in the Southwest, would wait for acorns to ripen and fall before collecting them. Other forms of harvest included the raiding of acorn woodpecker "granaries" (see Appendix 4), or rodent stores, usually in times of hardship or when travelling (Barrett and Gifford 1933; Bean 1972; Kniffen 1939).

The time of harvest was often under careful control. Hunters or foragers would report back to villages when the crop was ready, and the harvest proper would often be preceded by a first-fruit ceremony in which a small quantity of acorns were gathered, processed, and eaten, (e.g., Bean and Saubel 1972; Beals 1931). There might be severe social prohibitions on harvesting before the ceremony, and only after such ceremonies could the real harvest safely begin. Bean and Saubel (1972) recorded that harvest was timed to begin just before the winter rains, because acorns, either on the trees or on the ground, which got wet at this time of year, might split and rot. This would not necessarily ruin the harvest, but could mean more work as the black, rotten parts had to be cut out. The extent of ripeness of acorns was apparently also an important consideration, but opinions on this varied. Gifford (1932b) reported that the Yavapai collected fallen acorns, rather than knocking them from the trees. Apparently sweetness was of particular importance, as they only collected acorns of the relatively sweet *Q. emoryi*, and ignored the more abundant, but bitter, acorns of *Q. arizonica*, and would search amongst the trees until they found a particularly sweet specimen. Gifford noted that the Yavapai were aware of the fact that while green acorns were bitter, once they had ripened fully they might become sweet. The Wintu, who harvested at least five species of acorns, both relatively sweet and bitter, and harvested acorns from the trees, preferred green acorns, because these made a "nice smooth white sticky" soup, whereas ripe acorns collected from the ground "were less desirable because they made a 'dark soup'" (Du Bois 1935, 18).

Acorns were knocked from the trees by shaking, or beating with long poles, usually by men and boys (Beals 1931; Chesnut 1974; Dixon 1905; Gifford 1932b; Powers 1874).

Powers (1874) commented that "a tree which has been well stripped looks as if it has been scourged in a mighty hail storm". Sapir and Spier (1946) recorded "acorn-laden limbs" being chopped from the trees, and Chesnut (1974) reported that small branches would be cut off. Acorns might also be picked from low branches and shrubs (Sapir and Spier 1946). Inaccessible or intransigent acorns might be left on the tree until they fell (Goldschmidt 1951). The acorns would be picked up, generally by the women and children, though they might also be swept up with a branch and then brushed onto a flat basket, which was said to be quicker than picking them up individually (Gifford 1932b). The acorns would then be carried, usually in tall "burden-baskets" to the camp, where they would be spread in the sun to dry (Chesnut 1974; Sapir and Spier 1946).

3.2.1.3.2. Initial processing - the acorn camp

For those groups who travelled some distance to harvest acorns, drying of acorns would usually be carried out during the harvesting period. Thorough drying was apparently important, for both future use and storage, and probably also to reduce weight for transportation, if the acorn camp was not the main autumn and winter camp. Bean and Saubel (1972) noted that only if the rains began, would occupation of the acorn camp be cut short and the acorns carried back immediately to the main camp to be shelled and dried. Someone might be left in the acorn camp while others harvested to turn the acorns in the sun, and no doubt to prevent predation, as well as enabling the sorting out of insect-infested acorns which had been gathered (Bates 1983; Du Bois 1935). Shelling of some acorns might also be done at the acorn camp, and the whole group might gather in the evenings to carry out this task (see, e.g., Merriam 1918; Goldschmidt 1951). The shelled acorns might then be further sun-dried (Chesnut 1974).

3.2.1.3.3. Transport

In cases where the acorn camp was a temporary, seasonal settlement, large quantities of acorns would need to be transported back to the main winter camps. Carrying was done in large burden baskets, often by the women but sometimes with the assistance of others (Dixon 1905; Driver 1936; Kniffen 1939). Gould (1975) notes that Tolowa women would move constantly from oak grove camps back to the coastal villages during the harvest season, a distance which could be as much as from 5-15 miles. Because variable amounts of processing took place at the acorn camp the transported acorns could be in virtually any form - whole acorns in their shells, shelled acorns, or ground acorn meal (Bean 1972).

3.2.1.3.4. Drying

As Bean (1972) notes, aridity, at least in the southern part of California was a distinct natural advantage for the storage of food. Acorns always seem to have been thoroughly dried before storage. Sun-drying was common, but acorns might also be dried over fires in the houses, perhaps on racks slung from the roof or on frames (Driver 1936; Merriam 1918). Hudson and Blackburn (1983) describe drying granaries, as distinct from storage granaries, in which the acorns were dried before being shelled and taken indoors, and Gould (1975) notes that during periods of sunny weather acorns might be removed from storage and laid out to dry, preventing or retarding fungal or insect attack.

3.2.1.3.5. Storage

Some groups, especially outside California, only ate acorns in season and did not apparently store them in quantity (Chamberlin 1911), but storage seems to have been the general practice in California. Goldschmidt (1951) noted that half-ripe acorns in particular were stored, and Spier recorded that "green acorns", first shelled and then sun-dried, would keep longer than acorns gathered dry, up to five years. One reference (Kniffen 1939) notes that different species were stored separately, since they each had different qualities. Although this is not recorded elsewhere there are frequent references to the different uses for different species of acorns, so this practice of separate storage may have been fairly frequent.

Acorns were usually stored unprocessed, though in some cases they were removed from their shells, while in others they were left in them (Barrett and Gifford 1933; Goldschmidt 1951; McLendon 1977). Chesnut (1974) and Gifford (1932b) both recorded both shelled and unshelled acorns stored by the same people. Acorns could also be stored as ground meal or flour, and Kniffen (1939) and Driver (1936) recorded storage in all three ways by the Pomo and Wappo. The reasons for leaving shells on are often suggested to have been as a means to prevent predation, by insects particularly, and perhaps to stop them getting damp. However at least one reference suggests that shells were removed to prevent destruction by insects (Gifford 1932b). Duncan (1961) reported that dried, shelled acorns would be stored in granaries, with the remainder left outside during the rainy winter to "cure". They would then be shelled and put in granaries, presumably taking the place of those already eaten.

Storage often took place in the large characteristic granaries so frequently commented on by early visitors to California (see, e.g., Bates 1983), constructed usually of loosely-woven branches to permit air circulation and prevent the acorns going mouldy. The tops were

usually rounded or pointed, and covered with down-sweeping conifer branches or other vegetation designed to shed rain (Bates 1983; Kniffen 1939; Merriam 1918). Granaries were usually supported on several large posts, or on piles of rocks, and predation by rats, squirrels, ants, etc, might be further deterred by smearing the supports with pitch (Heizer and Elsasser 1980). Each house might have its own granary (Bean 1972), or there might only be one per settlement (Goldschmidt 1951). Granaries could also be fashioned from living bushes - their branches bent back and lashed into shape (Du Bois 1935). Sometimes they were in the form of baskets placed in trees (Merriam 1918; Bean and Saubel 1972), or just placed on the ground if there was little threat of rodent attack (Kroeber 1932). The Yana apparently included maple leaves in the granaries to assist in preservation (Sapir and Spier 1946), and the aromatic leaves of the California Bay (*Umbellularia californica*) could be added to stores to help deter insects, according to Heizer and Elsasser (1980). The Miwok added large quantities of "wormwood", which apparently acted as an insect repellent (Bates 1983).

Other methods of storage included burial in pits lined with skins, leaves, mats or bark (Du Bois 1935; Duncan 1961; Kroeber 1932); especially when temporarily leaving camp, or for reserve supplies when there had been a particularly good harvest (Beals 1931). Acorns might be kept in baskets or in skins (Goldschmidt 1951), sometimes inside the house (McLendon 1977), especially after the rains began (Hudson and Blackburn 1983). Occasionally acorns were just piled along the walls of houses (Kroeber 1932), or they might be stored in cedar-bark tubes (Beals 1931). The Apache collected acorns in sacks and then just left them as they were until required (Opler 1941).

Small quantities, especially of ground, and sometimes leached, meal might be kept in pottery ollas where these were made. Some acorns, usually in small quantities, might be stored in secret places sometimes in pots away from the camp, e.g., in dry caves or clefts in rocks for an emergency supply (Bean, 1972; Bean and Saubel 1972) especially along trails where they might be used by travellers.

A further method of "storage", which apparently served the purpose of simultaneously leaching the acorns, was to bury them in mud or water seepages, for anything from several months to years (Balls 1962; Du Bois 1935; Goldschmidt 1951; Gunther 1973). Merriam (1918) noted that acorns buried in mud were still apparently as good as ever after 30 years. Acorns have been recorded to keep for up to 5 years in granaries (Spier 1978). Heizer and Elsasser (1980) note that it was common to collect enough acorns to last for two years. Bean (1972) and Bean and Saubel (1972) noted storage of acorns by the Cahuilla from a year to several years. Duncan (1961), working with the Maidu, also reported that acorns could be stored for years, but that by April of the first year they would begin to taste old.

Seedlings of *Q. kelloggii* (the most commonly-used species) would be uprooted and the green cotyledons ground up and added to mush made of stored acorns to give it a fresh taste. Baked acorn bread could also be stored, as it kept for months (Du Bois 1935), and leached acorn flour could be formed into cakes and dried for storage, after which it would need to be reground (Bean and Saubel 1972). Such cakes was sufficiently well-preserved to be traded (Dixon 1905).

3.2.1.3.6. Acorn processing

Though acorns were sometimes eaten in other ways their most common use was as a flour, which would generally require leaching before being cooked into soup, mush, or bread. Considerable care seems to have been taken over all processing and cooking utensils and activities, and the cook might be judged by her ability in making acorn food that was of the correct consistency, sweetness, and colour, or considered "sloppy" if correct care was not taken of mortars (Bean and Saubel 1972; Duncan 1961). Though one report suggests that the amount of sand eaten with acorn foods (introduced during grinding or leaching) by the Indians was such as to have an extreme effect on the teeth, and Dixon (1905) comments that bread and soup could be gritty with sand or ash, this does not seem likely to have been very common, because of the emphasis on careful preparation. Certain species seem to have been preferred for particular foodstuffs, and differences between "green" and ripe acorns, as well as methods of preservation were apparently related to the particular method of preparation - whether roasted or boiled, or made into soup, mush or bread of varying kinds (Barrett and Gifford 1933; Dixon 1907; Du Bois 1935; Duncan 1961; Goldschmidt 1951; Kniffen 1939; McLendon 1977).

3.2.1.3.6.1. Shelling

Though acorns were sometimes shelled before storage this was often the first stage in daily food preparation. Shelling could be done using the teeth, or by splitting with a small rock, placing the acorns on another rock, sometimes with small hollows to hold the acorn (Barrett and Gifford 1933; Chesnut 1974; Dixon 1905; Du Bois 1935; Gifford 1932a, 1932b; Hudson and Blackburn 1983; Goldschmidt 1951; Spier 1978). Shelling by rubbing with a mano on a metate (Gifford 1932b), sometimes after roasting, while the shells were still hot and brittle (Opler 1941) is also recorded. The method used might depend upon characteristics of particular species, such as shell thickness (Barrett and Gifford 1933), or ripeness - the Foothill Yokuts used their teeth for green acorns (Spier 1978). Little is said in the literature as to the fate of the shells, though Barrett and Gifford (1933) noted that, though they might simply be discarded, they were sometimes burnt, because they produced

a hot and lasting fire. The bitter "skins" or testas might also be rubbed off the acorn before further processing (Dixon 1907; Goldschmidt 1951; Waugh 1987).

3.2.1.3.6.2. Flour production

There were several ways of producing acorn flour. In areas where there were flat outcrops of rock, bedrock mortars consisting of hollows made in the rock were used. Portable mortars were also used. In many cases these consisted of flat stones with shallow hollows, used in conjunction with basketwork hoppers, which might be fixed to the mortars with pitch, or just held in place by the feet (Chesnut 1974; McLendon 1977). Stone pestles were used in conjunction with all of these, and could vary from unworked pebbles picked from river beds to smoothed, shaped tools with incised designs. The metate and mano were also used for grinding (Drucker 1937), again these might be unworked flattened stones or might be more elaborate. Although stone tools seem to have predominated, there are reports of the use of wooden implements, ranging from mortars hollowed from oak (Kroeber 1932; see also Hudson and Blackburn 1983; Mayer 1976) to slabs of pine used as grinding surfaces/metates. Pestles and manos were usually of stone (Barrett and Gifford 1933; Dixon 1905, 1907; Du Bois 1935; Goldschmidt 1951; Powers 1874), though wooden pestles may also have been used (Hudson and Blackburn 1983).

The acorn flour would generally be sifted, or "winnowed" as it is often termed in the literature, using open-weave baskets, or flat trays on which the flour was shaken, to separate the coarse from the fine flour. The coarse particles could then be re-ground (see, e.g., Barrett and Gifford 1933; Beals 1931; Chesnut 1974; Dixon 1905, 1907; Driver 1936; Hudson and Blackburn 1983; McLendon 1977).

3.2.1.3.6.3. Leaching

Acorn flour seems always to have been leached to remove the bitter tannin. The most common method was to use a pit or hollow, which could be several feet across, scraped in sandy soil, and sometimes lined with leaves or basketry. The flour was placed in this and water poured over. The water could be cold, or might be heated first, and sometimes temperature was varied through the process. Leaching areas would often be situated near a stream or other source of water, as several applications of water were required, the process taking anything up to a day, and varying for acorns of different species (Barrett and Gifford 1933; Bean and Saubel 1972; Chesnut 1974; Dixon 1905; Du Bois 1935; Duncan 1961; Gifford 1932a; Goldschmidt 1951; McLendon 1977; Meigs 1939).

Leaching of small quantities of flour might be done in baskets lined with leaves (Barrett and Gifford 1933; Hudson and Blackburn 1983); and Dixon (1907) describes the construction of a small platform of sticks raised above the ground on which leaves and then sand were placed to form the leaching basin. A similar construction, on a platform supported by four poles, which appears to be about a metre above the ground, is pictured by Merriam (1918, 135). Leaching could also be done by mixing flour and water in receptacles such as baskets and wooden bowls, leaving to settle, and then pouring off the water (Hudson and Blackburn 1983).

Alternative methods of leaching acorns have been recorded. These included placing acorns in running water, in a net bag or basket, and leaving, usually for several days, until the tannins were sufficiently leached out. The acorns could then be dried before making into flour (Romero 1954). There is also a record of leaching acorns by placing them in hot springs, though this can not have been a very widespread practice (Hayes 1929, cited in Bean and Saubel 1972). Chesnut (1974) recorded one instance in which acorns were buried in sandy soil with grass, charcoal and ashes, and were then soaked in water from time to time until they became sweet.

3.2.1.3.6.4. Food production

Once leached, the damp flour could be removed from the sand basin by slapping a hand on it and lifting it up in one piece, with the sand then washed from the dough-like slab (Barrett and Gifford 1933; Dixon 1907). Chesnut (1974) alternatively reported that the central portion of flour would be scooped out of the leaching pit, so that it was entirely free of sand, and was used for bread. The remainder was mixed with water for soup, and any sand would settle to the bottom.

The production of "mush", or thinner soup, seems to have been the most common use of acorn flour, though it could also be baked into biscuits or bread. Bean and Saubel (1972) comment that the Cahuilla used fine grades of flour to produce bread, while coarse meal was used for acorn mush, while Du Bois (1935) recorded that flour was made finer for mush than for bread. Goldschmidt (1951) reported the use of "flour" as coarse as whole wheat for bread making.

a) Acorn mush

Mush or soup was usually cooked in baskets by "stone-boiling" - stones were heated in the fire and then added to the flour and water mix, sometimes after first rinsing off any ashes. The cooking required constant attention and stirring to prevent the stones burning the mush

or the bottom of the basket (Barrett and Gifford 1933; Bean and Saubel 1972; Chesnut 1974; Dixon 1905; Du Bois 1935; Goldschmidt 1951; Heiser and Elsasser 1980; Hudson and Blackburn 1983; McLendon 1977). Special stones which would not shatter with sudden heating and cooling were often selected for cooking (Dixon 1907), and might be kept from one cooking to the next (Goldschmidt 1951). Boiling stones, sometimes with holes in them for ease of handling, could be fashioned out of steatite, a soft stone, where this was available (Hudson and Blackburn 1983). Du Bois noted that women were "always on the lookout for suitable stones" (1935, 19). Where suitable stone did not exist substitutes might be made out of baked clay (Heiser and Elsasser 1980).

The mush or soup was often made of acorn flour alone (Heiser and Elsasser 1980), though Gifford (1932b) notes that it was always cooked with meat by the Yavapai, for whom acorns were not considered a staple food. Various seeds, greens, fungi, roots, berries or meat were sometimes added to alter flavour or consistency, and flour from different acorn species could be mixed to similar purpose (Barrett and Gifford 1933; Bean and Saubel 1972; Dixon 1905; Duncan 1961; Heiser and Elsasser 1980; Meigs 1939). Clay or ashes were sometimes added to mush to absorb any remaining bitterness (Dixon 1905; Heiser and Elsasser 1980). The mush could be eaten hot or cold. It had a firm, jelly-like, consistency when cool, and could be cut into squares, or eaten with the fingers or "spoons". Its colour could vary from pale pink, through tan, or reddish brown (Bean and Saubel 1972; Chesnut 1974), to "the colour of chocolate pie" (Romero 1954).

b) Acorn bread

Acorn bread or biscuits were made either on flat hot rocks next to a fire, or most frequently in an earth or pit oven. Barrett and Gifford (1933) also describe a "bread" made by placing hot acorn mush in a small basket into cold water, turning it into a gelatine-like "loaf". The earth oven consisted of a pit, usually lined with stones, in which a fire was lit. When sufficiently heated, the embers would be removed to expose the hot stones. The dough, usually wrapped in leaves, was placed in the pit, and covered with more hot stones. Dixon (1905) recorded the inclusion of a hot rock, wrapped in leaves, in the centre of the dough. Sometimes another fire was lit on top of the oven (Goldschmidt 1951), though the pit was more usually covered with earth to retain the heat, and would then be left for several hours, often overnight (Chesnut 1974; Du Bois 1935; Goldschmidt 1951). Flavourings as for mush and soup might be incorporated, and ash, or red earth or clay could be added to the flour and water mix before baking, said to sweeten it (Barrett and Gifford 1933; Chesnut 1974; Dixon 1905; Driver 1936; Du Bois 1935; Kniffen 1939). Driver (1966) recorded that damp flour was stored for ten days before baking to allow it to ferment. The bread is described as fairly solid and heavy (Dixon 1905), and of a rich, greasy consistency (Du

Bois 1935). It was often dark brown or black in colour, though bread made without clay was lighter in colour (Chesnut 1974), and a "white" bread is described by Barrett and Gifford (1933). Chesnut (1974) reported that acorn bread, made with or without clay, was very sweet, probably because of the prolonged cooking. Goldschmidt also noted a bread made of fresh, ripe unleached acorns, which was "'neither sweet nor bitter', but had a distinctive taste" (1951, 416). Chesnut (1974) also recorded that bread could be made by building a fire over the flour while still in the leaching pit, but that this was said to produce bad bread. Sand would stick to it, and oil in the acorn flour passed away into the sand as the bread heated up. Bread could also be made of "molded" acorns, pounded into a coarse meal (Du Bois 1935), and might have a "bitter tang" (Goldschmidt 1951). It is not clear whether these are the same acorns as those "stored" in mud (see above), or whether another process was used. Du Bois (1935) noted that acorns of one species left in mud to "mold" were not pounded into flour, but would be subsequently soaked with pine needles to sweeten them, and then boiled into a lumpy soup. "Molded" acorns of another species were used for bread, the "moldier" the better.

c) Other acorn foods

Some acorns, particularly those which had been previously buried in mud, were boiled or roasted in fires (Dixon 1907; Du Bois 1935; Goldschmidt 1951; Gunther 1973). Goldschmidt reported that they "taste a little sulphurlike" (1951, 413). Duncan (1961) reported that "dark coloured" acorns would sometimes be immersed in a stream for a week, boiled, and then eaten salted. Some sweet acorns were eaten roasted, and some even raw (Goldschmidt 1951; Gunther 1973). McLendon (1977) recorded that sweet acorns would be boiled in their shells until they cracked, the shells peeled off, and then eaten. Opler (1941) recorded that the Apache would sometimes roast acorns before shelling, then pound them up and mix them with meat and fat to form a kind of "pemmican" which could be stored and was ready to eat.

3.2.2. Eastern North America

3.2.2.1. Acorns in the subsistence system

Any cursory examination of the ethnography of eastern North American Indians would suggest that most groups placed an over-riding reliance on the agricultural crop of maize, often stored in large quantities, with major contributions to the diet from other cultivated plants (mainly beans and various cucurbits), hunted animals and fish, but apparently with little reliance on wild plants (see e.g., Trigger 1978). Driver (1953) commented that, in contrast to California, wild game and fish were more important than wild plants, and that

these were generally resorted to in quantity only when the maize crops failed (see also Heidenreich 1978; Trigger 1969). Salwen (1978), however, commented that accounts of early observers did not stress wild plant foods, and that they were probably more important in the subsistence system than they might seem. Feest (1978b) noted that the principal subsistence of the Virginia Algonquins was hunting, fishing, and gathering, and estimated that horticulture made up only around 25% of the diet; while Fenton (1978) comments that, though the Iroquois are generally known as horticulturalists, hunting, fishing, and gathering of wild plants occurred, and it was difficult to estimate the actual balance of the various resources from available sources. Swanton (1946) cites many examples showing that the stored maize crops of the various peoples of the Southeast did not generally last from one harvest to the next, and were not expected to, so that it was a normal part of the subsistence pattern to turn to wild plant foods, often acorns, during part of the year. Hudson (1976) cites the example of the Seminole, who objected strenuously when asked to move from their original lands because oaks, hickory, and persimmons, without which they felt they could not survive, were absent from the new lands.

Apart from the writings of early travellers, information on use of acorns and other wild plants is available in the form of several ethnobotanies, mainly compiled in the early years of this century. The potential for, and perhaps interest in, ethnographic recording of wild plant use was apparently smaller here than in California, and these studies rarely provide the wealth of detail regarding methods of plant use recorded there. The importance of wild food plants is however emphasied by their continuing use after an acculturation process that occurred earlier and was more severe than that in the west (see, e.g., Fenton 1978).

Acorns are certainly less emphasised in the literature than in California, and it is plant foods such as hickory nuts, and, in the north, wild rice and maple sugar which have received most detailed attention, perhaps because their processing involved relatively complex technology and sequences of events. Nevertheless, the use of acorns is probably mentioned as often as that of hickories (see e.g., Swanton 1946, 293, Table 2), and Smith (1932) noted that all the Ojibwe he encountered told of their former dependence on acorns. Driver (1953) commented that in the Southeast acorns were second only to hickory nuts as a source of oil (see also Swanton 1946). A role for acorns which has often been emphasised in the east is as a food supply during crop failures, or at other times of need. Such a role rarely seems to be mentioned so frequently for other specific wild plant foods, and, for example, does not seem to have been a role for hickory nuts (see e.g., Driver 1953; Merriam 1918; Rogers 1978; Trigger 1969; Waugh 1916; Williams 1827, cited in Gifford 1936; Zeisberger 1885).

It is generally difficult to ascertain whether "sweet" or "bitter" species were preferred. Smith (1923, 1932) noted that during "aboriginal" times all kinds of acorns were used, and the Forest Potawatomi used "all kinds of acorns indiscriminately" (Smith 1933, 100). Gilmore (1919) describing uses of plants by Indians on the western fringes of the Eastern Woodlands, where *Q. macrocarpa*, which is recorded by Densmore (1974) as "sweet", and *Q. rubra* were present notes that the latter species especially was used, after lye treatment. *Q. rubra* was also described as a favoured species by Smith (1932), because of its large size and abundance, and despite the fact that it was more bitter than *Q. alba*. Waugh (1916, see also Fenton 1968), and suggested that it was probably the sweeter species (such as *Q. alba* and *Q. prinus*) which were used more frequently by the Iroquois, though *Q. rubra* and *Q. velutina* might be used in times of necessity. Zeisberger (1885, 1:128) noted that the Chippewa used "the worst sort of acorns". Hudson (1976) noted that the sweeter *Q. virginiana* was eaten where it occurred along southeastern coasts, but other more bitter species, including *Q. stellata*, *Q. alba*, and *Q. prinus* were used in the interior.

3.2.2.2. The harvesting/processing sequence

3.2.2.2.1. Harvesting

There do not appear to be any detailed descriptions of the acorn harvest, or that of other nuts, in the east. For rice and maple sugar harvesting whole family units seem to have been involved, and a separate camp was often set up (see, e.g., Densmore 1974; Waugh 1916). Generally, subsistence-related movements were from semi-sedentary summer settlements with permanent structures situated among the agricultural fields, to winter hunting camps, often at some distance in "deep forest" (Swanton 1946; Trigger 1978). Movements tended to occur in late autumn or early winter. In some cases winter camps would be visited mainly by the men, leaving most of the women behind (Fenton 1978), in others whole villages would move from the fields into the woods (Callender 1978; Ritzenthaler 1978; Salwen 1978). Heidenreich (1978) commented on the location of autumn and winter hunting camps in the main acorn-producing areas, where animals such as deer, and many smaller mammals would congregate, and this seems likely to have been generally the case. Whether acorns were themselves a target of these seasonal movements, however, is not apparently recorded.

Harvesting of acorns, along with other plant gathering, is usually described as an activity of women alone, occasionally with older men and children (see, e.g., Densmore 1974; Feest 1978b; Fenton 1978; Ritzenthaler 1978; Waugh 1916). Waugh (1916) noted that nuts were gathered after they had been brought down by the frosts, though chestnuts are recorded as being eaten when "green", and Smith (1923, 1932) noted that hazelnuts were

preferred in the "milk" or soft stage, which implies that they were picked before they fell to the ground, but it is uncertain in what way acorns were collected.

3.2.2.2.2. Storage

There are few specific references to storage of acorns, though they are sometimes described as an important food during the lean spring of the year. Smith (1907, cited in Swanton 1946) noted that acorns were a principal food of the the Indians of Virginia during May and June. Both cultivated and wild plant foods were often dried in large quantities for storage, and there are some references to drying acorns (e.g., Smith 1932; Smith 1907; cited in Swanton 1946). Sun-drying, sometimes on purpose-built drying-racks, seems to have been the most common method used for maize and other products, and has been recorded for acorns (Smith 1933). "Smoking" is also recorded as a method of drying and preserving plant foods (Clifton 1978), and the use of fire was common (Fenton 1968; Swanton 1946). Hariot (1893, cited in Swanton 1946) recorded that acorns were dried on hurdles made of reeds, with fire underneath. The Ojibwe and Forest Potawatomi stored whole acorns after they had been leached (Smith 1932; see also Driver 1953). Storage of plant foods often seems to have taken place in underground pits (Waugh 1916), often lined with bark or grass (Fenton 1968) though storage "bins" or other overground structures are also described (Feest 1978b). Densmore (1974) recorded that sweet acorns gathered in late autumn would be buried in the ground for use in winter or spring. Other methods of storage for foods included pottery or bark containers (Clifton 1978).

3.2.2.2.3. Acorn processing

The usual method of ridding acorns of tannins seems to have been by boiling them in water, sometimes changing it several times (see, e.g., Fenton 1968; Smith 1923, 1932; Trigger 1969; Waugh 1916). The vessels in which boiling occurred are rarely described, though Waugh (1916) noted that cooking in general was done in ceramic pots, wooden vessels, or even holes in the ground to which boiling-stones were added; and the use of birch-bark containers for boiling sugar maple is well-documented (see e.g., Densmore 1974).

3.2.2.2.3.1. Shelling

The shells usually seem to have been removed prior to this process. Cracking of nut shells was usually done using one flat stone placed on the ground, and another held in the hand. These could be just naturally flattened pebbles, or special stones with depressions to hold the nuts (Fenton 1968; Smith 1907, cited in Swanton 1946; Waugh 1916). Significant

differences between stones used for cracking acorns or for cracking the hard-shelled hickory and walnuts do not appear to be mentioned. Smith (1923) records that the Menomini would parch the acorns and then flail off the shells, though the precise way in which this was achieved is not described.

3.2.2.2.3.2. Leaching

The precise process of tannin removal varied. Sometimes a lye, made of ashes and water, was used to neutralise the tannin. Smith (1933) recorded that the ashes of hardwoods were used, and basswood (*Tilia*) seems to have been the preferred species, as it was for the lye used in maize preparation (Gilmore 1919). Parker (see Fenton 1968) recorded that acorns were boiled in lye, or roasted in ashes, and then required several washings. Smith (1923) recorded that the Menomini first boiled the acorns until they were almost cooked, after which the cooking water was thrown away. The acorns were placed in a net, in more boiling water to which ashes had been added, and simmered to rinse off the lye. The Ojibwe and Forest Potawatomi soaked acorns in lye as a preliminary stage. The acorns, in a woven bark bag, were then washed in several changes of warm water (Smith 1932, 1933).

It is uncertain whether variations in treatment related to the acorn species used. Though Smith stated that *Q. alba*, a relatively sweet species, did not require lye treatment, he nevertheless described it being used for this species, by both Ojibwe and Menomini (Smith 1923, 1932). Other species, including *Q. macrocarpa*, *Q. rubra* and *Q. velutina* were described as more bitter, though after lye treatment became equally sweet. Densmore (1974) recorded several methods of preparation, none of which involved the use of lye, for the "sweet" *Q. macrocarpa*. Gilmore (1919) noted that lye treatment was necessary for acorns of *Q. rubra*, and though acorns of the generally sweeter*Q. macrocarpa* were also used it is unfortunately not clear whether lye treatment was needed for these.

Although boiling in water seems to have been the most commonly recorded method of leaching, Bushnell (1909) observed that the Choctaw of Louisiana first pounded acorns in a mortar, and then leached them in an openwork basket with several applications of water, a method apparently similar to that used in California.

3.2.2.2.4. Food preparation

Once leached, acorns could be eaten directly, while still more-or-less whole, often cooked with other foods. Parker (see Fenton 1968) recorded that leached acorns were pounded in a mortar, and then mixed with maize meal or meat and made into soup or "pudding".

Alternatively they could be dried, sometimes by roasting, and stored at this semi-processed stage, and then removed for further processing when required (Driver 1953; Smith 1932).

3.2.2.2.4.1. Flour production

Processing of dried acorns usually required pounding into flour. The mortar and pestle seems to have been the most common means of producing acorn flour (Gifford 1936; Smith 1923, 1932; Fenton 1968), and the tools usually seem to have been the same wooden implements as the ones used for processing maize or wild rice (see for example Densmore 1974; Driver 1953; Trigger 1969). Stone implements, usually grinding stones and handstones, were used in the region for the grinding of maize (see, e.g., Waugh 1916), but it is not certain whether these were used for acorns. These could be simple unmodified flat stones. Smith (1933) noted that where suitable stone was available acorns were ground in mortar-like depressions in rocks, with stone pestles.

Smith (1923) observed that acorn flour was sifted, using a birch-bark container, before further use, so presumably some care was exerted to achieve the correct grade of flour, as is so commonly recorded in California.

3.2.2.2.4.2. Acorn foods

Acorn flour seems most frequently to have been made into, or added to, soups, or mush (Smith 1923, 1932, 1933; Fenton 1968; Zeisberger 1885). These were often mixed or flavoured with other ingredients, such as bear oil (Smith 1923), blueberries or maple syrup (Smith 1932), maize flour or meat (Fenton 1968; Driver 1953). There are some reports of the use of acorns in bread, apparently as the sole ingredient, but the precise process is not described (Driver 1953; Feest 1978a, 1978b; Hariot 1893, cited in Swanton 1946; Romans 1775, cited in Swanton 1946; Smith 1907, cited in Swanton 1946; Waugh 1916). Waugh also recorded one informant who said that any nut except acorns would be mixed with maize flour to make bread. Swanton (1946, 367) cites the example of a party of shipwrecked Spaniards on the southeastern coast who were offerred "lumps of acorn cake, yellow and red, which are rough and bitter".

There are also references to the use of acorns as a source of oil (DeOviedo 1973; Harper 1958; Lawson 1860; cited in Swanton 1946; Hariot 1893, cited in Swanton 1946; Hudson 1976; Swanton 1946) usually as a food, but also for "anointing" (Smith 1907, cited in Swanton 1946). In most cases it seems to be the acorns of the "live oak", *Q. virginiana*, which occurs only along the southeastern coasts, which was used for this purpose, though Hariot noted the use of "three kinds". Unfortunately the references to this method of

processing are sometimes rather ambiguous, so it is not always posssible to tell which types of nuts are referred to. The method appears to have been much more widespread for hickories, and is also recorded for walnuts (but see Reidhead 1976 and Talalay *et al.* 1984 on the improbability of this). The nuts, including shells, would be roughly pounded, and the whole boiled in water, with oil rising to the surface to be skimmed off (Talalay *et al.* 1984; Waugh 1916). Lawson (1860; cited in Swanton 1946) recorded that acorns were boiled until the oil rose to the surface. This was preserved, while the acorns themselves were eaten with meat.

Other ways of eating acorns are also recorded. Densmore (1974) noted that the Chippewa cooked sweet acorns by boiling them in the shell, splitting, and eating as a vegetable, or by boiling the kernels, mashing, and eating with grease (see also Tantaquidgeon 1942). Some, especially those reported to be "edible" or "sweet", were roasted (Densmore 1974; Gifford 1936; Harper 1958; Tantaquidgeon 1942). Smith (1923) recorded that the Menomini roasted and ground acorns of *Q. ellipsoidalis* to make "coffee".

3.2.3. Mexico and Central America

Little information is available regarding the use of acorns in this region. Other than those species which overlap with the United States, and have been recorded as food there, species of this region are rarely included in compilation volumes of plant uses (e.g., Hedrick 1972; Howes 1974) though Uphof (1968) records the use of *Q. reticulata* as a coffee substitute in San Luis Potosi, Mexico, and Tanaka (1976) records acorns of *Q. castanea* as "edible". The relevant volumes of the Handbook of Middle American Indians (Vogt 1969) emphasise the agricultural basis of subsistence of the native peoples of this region from the time of European contact onwards, and gathering of wild plants is referred to rarely, and then as being of limited importance. Acorns are mentioned only once as human food, and that by people in Baja California. Acorn use does not appear to have been recorded in any detail by early Europeans. Merriam (1918) commented that in Mexico acorns formed an important indirect resource, as food for the introduced domestic pigs, and this seems to have been a common role for acorns as far south as Colombia (Smith 1929).

Nevertheless, acorns have been recorded as human food in this region, though unfortunately with insufficient detail to allow any estimate of their importance, or of methods of their use. Merriam (1918) stated that in parts of Mexico acorns were sometimes eaten. Especially in northwestern Mexico, bordering on the United States, species including the sweet *Q. emoryi* are still gathered, sometimes commercially. They apparently fill the role of a snack food or delicacy (Bainbridge and Felger 1989; Smith 1929),

probably with methods of usage much as have been recorded in adjacent areas of the United States - New Mexico, Arizona, Nevada, etc., as described in 3.2.1.

Slightly further to the south the Tarahumar and Tepehuan Indians, inhabiting the northerly portion of the Sierra Madre Occidental were recorded by Pennington (1969) as using at least eleven species of oak, some of which include those used in the southwestern United States. Acorns were generally eaten with little preparation other than toasting on a "comal", though acorns of *Q. arizonica* were incorporated in maize flour tortillas by the Tepehuan after cooking, rinsing and crushing. Both groups are agriculturalists, though they utilised, until at least the 1960's, a large number of wild plants and animals, and owned domestic animals including pigs. Pigs generally foraged for themselves, and acorns of four species were thought of as especially good pig food by the Tepehuan, one of which was also used as human food.

The role of acorns through the remainder of the region is more uncertain. Beals (cited in Gifford 1936), who studied several western Mexican tribes in the early part of this century could find no evidence of acorn consumption, despite the presence of numerous oaks. The lack of emphasis on the role of wild plants by most ethnographers of the region has been noted by Javier Caballero and Cristina Mapes (1985). There is a considerable and growing focus on the ethnobotany of Mexico in particular, with the result that the importance of the role of wild plants in the subsistence of the region is becoming more emphasised, but many studies have only developed in detail from the 1970's onward (De Tapia 1990). Most studies have focussed on wild plant use by people in the mountainous districts of southern Mexico, such as Michoacán and Oaxaca, where numerous species of oaks often dominate in the hills, and though a very extensive use of wild plants has been demonstrated, the use of acorns at present is not recorded by many of these studies (Berlin *et al.* 1974; Javier Caballero and Cristina Mapes 1985; Messer 1978; Wilken 1970), though Gonzalez and Labat (1987) record the use of *Q. candicans* as food, and of *Q. rugosa* as a coffee substitute in Michoacan. Messer (1978) noted that most local people classified acorns as "not edible", though one man had observed roasting of acorns when a boy, and others had heard that acorns were gathered for food in some of the mountain villages. Javier Caballero and Cristina Mapes (1985) also noted that older people recalled eating tortillas of maize mixed with acorn flour during the Mexican Revolution of 1910-1917.

3.2.4. Europe, excluding the Mediterranean

3.2.4.1. Introduction

Across Europe in historical times, there are records of acorn use by people, as well as of their role as food for pigs, particularly important in Mediaeval times. Maurizio (1927) and Vencl (1985) collected together many of these references, but little of the information relating to human consumption is very detailed.

3.2.4.2. Acorns in the subsistence system

In Europe acorns are usually reported as a food resorted to by people only in times of famine (e.g., Braudel 1981; Brockmann-Jerosch 1986; Burkill 1935; Clark 1952; Maurizio 1927; Meirion-Jones 1982), and with the exception of the sometimes sweet acorns of *Q. ilex* (which occurs in the southern part of the region and is discussed further in 3.2.5.), have usually been characterised as unpalatable, if not poisonous, as they are often thought of by people in the region today. Braudel (1981, 112) in a review of the eating habits of Europeans from the fifteenth to the eighteenth centuries commented that "consumption of 'acorns and roots' as in Dauphiné during the winter of 1674-6 was quite abnormal, and a symptom of terrible famine", continuing "Lemery incredulously reported in 1702 that 'there are still places where these acorns are used for the same purpose'".

There are certainly numerous reports of the use of acorns, especially during periods of hardship, throughout Europe, and the practice may not have been as "abnormal" as Braudel suggests. In the eight century the Bishop of Metz, in eastern France passed a law requiring bishops to ensure a supply of acorns to the populace in years of food shortage (Maurizio 1927). Acorn bread, ground from roasted acorns, was recommended as a health-giving food by thirteenth-century Welsh physicians (Loewenfeld 1957). Brockmann-Jerosch (1986) states that in France in 1548 acorn bread was eaten "out of necessity", as it was in Westphalia during wartime in 1759. He also cites a "legally approved famine bread" of "more recent times" in Russia, consisting of 2 pounds of rye flour, two pounds of rye bran, and 10 pounds of acorn flour. In England as well the use of acorns has been recorded during periods of food scarcity (Merriam 1918), and Clark (1952) cites Harrison, writing in 1586 that acorn bread was made at such times, and was eaten especially by the poorest people. Burkill (1935) noted that bread made of the acorns of *Q. robur* was "detestable", but was said to have been used at times in large quantities.

Acorn flour was being produced for human consumption in the mill of the monastery of Sindersdorf in Upper Bavaria as late as 1604 (Brockmann-Jerosch 1986). In both eastern

and western Europe in the sixteenth century acorns were amongst the items required in tribute by landowners, though it is not stated whether these were required by the landowners or their livestock (Maurizio 1927). Maurizio also cites references to the use of acorn bread in France and Russia in the eighteenth century, and says that acorns were commonly eaten and made into bread in eighteenth-century Germany. Acorn bread was used in Norway and the south Tirol in the nineteenth century. He also cited information from a Polish botanist suggesting that in parts of Poland, at the time of writing, acorn flour was so normal an ingredient of bread that loaves made purely from cereal flour were virtually unknown. Braudel (1981) commented that in the fifteenth to eighteenth centuries "chestnuts" often filled the role later occupied by potatoes in parts of France, and that in Aquitaine they were known as "ballotes", which is a term more commonly associated with acorns. Whether these were acorns or chestnuts is uncertain, though Meirion-Jones (1982, 326) quotes reports from nineteenth-century Brittany of the use of both chestnuts and acorns "by the lower orders". Acorns were collected for human use on a large scale in Germany during the First World War (Maurizio 1927), and Loewenfeld (1957, citing Scheerer 1948), recorded that acorn flour was at that time used commercially in Germany, and was permitted to make up a third of the total flour used for certain purposes.

Brockmann-Jerosch (1986) suggested that acorns were an important human food until at least the Middle Ages, citing various prohibitions against felling of, or damage to, oak trees, as well as requirements to plant oaks. He also noted that (unspecified) plant books of this period distinguished many kinds of oaks, now combined into two species (*Q. petraea* and *Q. robur*), and indicated whether acorns of each kind were sweet or bitter.

To what extent acorns were used as food in Mediaeval Europe is uncertain, but the importance of acorns as a food for domestic animals, especially pigs, during this period is well known. Thus in Domesday England and Carolingian Germany land was often valued in terms of its ability to produce oak mast (Brockmann-Jerosch 1986; Grigson 1982; Rackham 1980), and the importance of acorns in subsistence at this time is therefore linked with the importance of the pig as a provider of food (see Loewenfeld 1957). The "Saxon Chronicle" of twelfth century England (cited in Loewenfeld 1957) recorded famines when oak crops failed, because of the reliance on pigs as a winter food. However, surprisingly little detail is known regarding the practice of pannage (Grigson 1982). In ninth-century Kent pigs were apparently driven to seasonal autumn settlements in the most favourable areas. Generally pigs would be allowed to forage for themselves, under the guidance of herders, and there are Mediaeval pictorial records of swineherds knocking down acorns with poles or sticks thrown at the trees (see, e.g., Longnon and Cazelles 1969). In later centuries pigs seem to have been fed in pens more frequently, often on agricultural products (Grigson 1982), though it is uncertain whether acorns were collected for feeding.

However, in parts of Britain in this century acorns were collected for stall-feeding of pigs (Howes 1948; Jones 1959; Ministry of Agriculture and Fisheries 1940), though they were also allowed to forage for food. In the New Forest and the Forest of Dean pannage was practiced until quite recently (Grigson 1982).

3.2.4.3. The harvesting/processing sequence

Methods of harvesting acorns for human consumption, or methods of storage do not appear to have been recorded in Europe. There are a few reports regarding the types of food produced from acorns, but there are few details which enable any processing sequences to be reconstructed.

3.2.4.3.1. Food preparation

Most of the reports of acorn use in Europe mention the use of acorn flour to produce bread (Brockmann-Jerosch 1986; Clark 1952; Maurizio 1927). The use of a mechanical mill, presumably normally used for grinding cereals, to produce acorn flour in Bavaria during the seventeenth century has already been mentioned (3.2.4.2.). Leaching of acorn flour is not often discussed, though Burkill (1935) noted that washing acorns of *Q. robur* in water, or burying them in soil, could lessen the bitterness. During the French famine of 1709 acorns were steeped in water before being used to make bread (Loewenfeld 1957). Merriam (1918, 136) recorded that in England and France acorns were boiled "as a substitute for bread", and Meirion-Jones (1982, 326) noted that acorns eaten in nineteenth-century Brittany "had some nutritious quality when boiled with milk". The fullest description of preparation of acorns within the region derives from its easternmost borders, in a report by Krünitz (1788, cited in Maurizio 1927), who noted that at the time of writing the Tartars of the Crimea lived on acorns and acorn bread. Acorns were dried and parched. Then, presumably in the form of flour, they were mixed with calcareous water to produce a porridge or mush. They were also pounded up, and mixed with cereal flour, in proportions of a half or a third of the total, to make bread, which was described as agreeable and nutritious, if a little doughy.

The use of acorns, especially of *Q. petraea* and *Q. robur* as a coffee substitute, has been recorded (Gassner 1973; Loewenfeld 1957; Mabberley 1987; Maurizio 1927; Tanaka 1976), and they are now included in some commercially-available non-caffeine coffee alternatives (personal observation); and in thirteenth-century Wales malted acorns were recommended for the production of ale (Loewenfeld 1957).

3.2.5. The Mediterranean

3.2.5.1. Acorns in the subsistence system

The earliest ethnographic record of human consumption of acorns in the Mediterranean comes from the writings of Greek and Roman authors of Classical times. The writings on this subject of Hesiod, Heredotus, Homer, Lucretius, Ovid, Pausanias, Pliny, Strabo, Theophrastus, and Virgil among others are frequently referred to on the literature on human use of acorns (see, e.g., Brockmann-Jerosch 1986; Brouk 1975; Clark 1952; Daubeny 1865; Driver 1953; Frazer 1913; Gifford 1936; Howes 1948; Loewenfeld 1957, Maurizio 1927; Soyer 1853; Vencl 1985). Classical mythology accords acorns a primary role in subsistence in a past "Golden Age", but most of the Classical and later references appear to refer to acorn eating as a more marginal practice, often carried out in remote or mountainous districts. Younker (1989), for example, cites Pliny's suggestion that it was only when there was an absence of cereals that acorns were used for bread. Strabo, however, wrote that acorns formed the main food in mountainous districts of northern Spain for two-thirds of the year (Clark 1952; Clark 1986). Usai (1969) cites Prudentius' comment that acorn bread was imported into Rome from Sardinia when there was a shortage of grain. Maurizio (1916, cited in Brockmann-Jerosch 1986, 90; 1927), noted that, at the time of writing, in central and southern Italy, Sicily and Sardinia "the farmers are forced to eat acorn bread during the winter months". Brouk (1975) noted that acorns were still used for bread making in southern Italy, in areas where the soil did not yield good cereal crops and the populace was too poor to buy cereal flour.

As Lewthwaite (1982) notes, reports do not generally provide enough detail to determine whether acorns were commonly used or only resorted to in times of famine. However, the available evidence suggests that use of acorns throughout the region may have been quite common until fairly recently. Bainbridge records that acorns were widely used in Spain, Portugal, Algeria, Italy and Greece during the 1800s (1985b; see also Loudon 1907, cited in Smith 1929). Memmo (1894, cited in Chesnut 1974) calculated that at the time of writing sweet acorns constituted 20% of the diet of poorer people in Spain and Italy. Altheer (1857, cited in Gifford 1936), and many others (cited in Usai 1969) recorded acorn "bread" as a daily food in Ogliastra, Sardinia, and this situation continued until around the beginning of the twentieth century, more recently mostly as a special food eaten mainly at festivals (Lewthwaite 1982; Maurizio 1927; Usai 1969). Acorn "bread" made in one village was also sold to other villages (Angius 1840, cited in Usai 1969). Even as late as the second world war some families had made a bread of acorns, cereal flour, and yeast (Usai 1969). In the 1960's Parsons (1962) recorded that acorns were still used by poorer people in Spain, especially in times of scarcity, and acorn bread has apparently been made by

some people in southern Spain within living memory (L. Peña Chocarro pers.comm.). The use of sweet acorns as a prized food around the Mediterranean was recorded by Merriam (1918), with some varieties considered superior to chestnuts; and Gifford (1936) quotes Ford's (1851) description of acorns as a delicacy eaten by high-ranking ladies at the opera in Madrid. Smith (1929) recorded eating acorns roasted like chestnuts in Portugal and Majorca, and similar use seems to have continued on Rhodes until at least the 1930's (Gifford 1936). Acorns were sold on a similar basis to chestnuts in Iberian markets (Howes 1948; Parsons 1962; Smith 1929) and are still sold on markets in Cadiz, Spain (T. Holden, pers. comm.), and in North Africa (Bainbridge 1987), where their use, up to the present day, has been frequently recorded (Bainbridge 1985b; Brockmann-Jerosch 1986; Howes 1948; Loudon 1905, cited in Smith 1929). Sweet, oily acorns have been traded from Morocco to Spain (Morris 1927). Smith (1929) noted that grafts of sweeter varieties had been made for some centuries, and were sold commercially in Majorca and parts of Spain. Parsons (1962) cites references to the Arab chroniclers of Mediaeval southern Spain, who recorded the fine quality of acorns, as well as the trouble taken by the natives to tend trees, and even to plant *Q. ilex* trees in gardens, irrigate, and fertilize them with dung, though it is unclear whether this was for human or animal consumption.

Most commentators have assumed that the species used have always been the sweeter acorns, as these are sometimes specified (Brockmann-Jerosch 1986; Chesnut 1974; Merriam 1918). However, the actual species used, both in Classical and later times, are by no means clear (see, e.g., Daubeny 1865; Hedrick 1972; Maurizio 1927). It is interesting in this respect to note that the names "*esculus* "or "*esculenta*" have been applied at various times to at least four species, none of which is *Q. ilex*, and only one of which is a supposedly more "edible" evergreen species. *Q. suber*, which is not generally referred to as sweet, is also recorded to have been eaten (Hedrick 1972; Remlinger and Charrier 1931, cited in Puntambekar and Varma 1934).

3.2.5.2. Acorns and pigs in the Mediterranean

Acorns have also been an important indirect food source, via the pig, in parts of the Mediterranean, especially in areas of Spain and Portugal, as well as on Corsica and Sardinia (Bainbridge and Felger 1989; Lewthwaite 1982; Mazuelos Vela *et al.* 1961; Parsons 1962; Smith 1929). Acorn-fed pork is also said to have been especially favoured in Italy (Bainbridge 1987). Parsons suggests that the antiquity of the "acorn-hog economy" extends at least as far back as Classical times, based on Greek and Roman references to the importance of the Iberian oaks for winter-fattening of pigs. Pigs, until very recently, seem to have been valued primarily for their fat content, and acorns were ideal fattening food (Parsons 1962; Smith 1929). Parsons estimated that in the 1950's and 1960's nearly a third

of Spain's pork was acorn-fattened, and described the process. In the Estremadura region of Spain pigs, either in small numbers from local villages, or en masse from the late summer fairs, were brought to the "dehesas" (oak parkland which had often had a cereal of legume crop understory) by swineherds. They would begin each day's feeding at the most distant part of the dehesa and finish up on the sweetest acorns and those closest to their sleeping place to ensure maximum weight gain. Sometimes the acorns were knocked from the trees with the aid of long poles to which a short stick on a cord had been attached, but this was considered detrimental, especially to the cork oak trees. Trees would be pruned in spring, partially to improve yields, and partially for charcoal producion, and ideal spacing for growth was achieved by thinning, with trees yielding fewer, or more bitter, acorns selected against.

In Portugal Smith (1929) noted that ideal production of both cork (from *Q. suber*) and acorns (from this species and *Q. ilex*) was achieved by thinning of trees, simultaneously permitting growth of forage for sheep and goats. The land was usually rented to pig-owners for the period when acorns were on the ground. Pigs were kept until the age of one and a half to two years, brought to the oak trees to fatten for three months, and then slaughtered. Smith also recorded that despite the commercial importance of cork from *Q. suber*, the greater productivity of acorns by *Q. ilex* was such that they were equally valued. Trees of *Q. ilex* were allowed to grow where they appeared in the fields, and arable cultivation or pasturing would take place around them.

Parsons (1962) noted that pig-rearing was also important, though on a smaller scale, in the mountains of northern Spain, where the practice of "montanera" or pannage was less common. Here acorns were harvested by hand for feeding to pigs, as well as cattle. Smith (1929) also recorded the small-scale collection by hand of acorns in southwestern Spain and Portugal, to be sold as pig feed.

3.2.5.3. The harvesting/processing sequence

3.2.5.3.1. Harvesting and storage

There are few references to harvesting of acorns in the Mediterranean region. However, one account of acorn use by the tenth-century Arab/Spanish author, Al-Awam, reported that acorns should be collected when fully ripe, and when they had taken on a black tint (Clément-Mullet 1977). It is not clear whether the acorns were picked from the trees or the ground. This account also provides one of the few detailed discussions of storage practices in the region. Al-Awam noted that special care must be taken to spread acorns in an airy sunny position as soon as possible after collection. If they were covered or piled up they

would very quickly, even overnight, spoil - heating up, staining black, and decomposing. Acorns should be turned several times throughout the day, until drying was complete. He noted that acorns might be exposed briefly to the sun, and then placed in containers, with the openings well-sealed with clay. Acorns would keep until May of the following year. They could also be dried by "smoking" on a rack of reeds or branches placed over a fire, removed from their shells, and stored. Al-Awam also provides one of the few accounts of shelling of acorns, in this case of acorns stored in their shells. They were removed from storage and placed in a bag or basket, then hit carefully with a mallet, apparently en masse, though how shells were then separated from kernels was not described.

3.2.5.3.2. Food preparation

In the Mediterranean acorns seem most commonly to have been utilised in the form of "bread", or were eaten roasted. Pliny wrote that acorn kernels were parched, and a flour was then milled into a paste which served as bread (Gifford 1936). According to Strabo, in mountainous Spain acorns were dried, "bruised' and then ground into a flour to make bread (Clark 1952; Clark 1986). Al-Awam (Clément-Mullet 1977) recorded that in tenth-century Spain whole acorns were boiled lightly in water, then dried. The shells were then removed, and the acorns were made into flour, from which a bread was produced. Clark (1986) reported that in northern Spain acorns were dried and milled into flour from which bread was made. This bread could be stored for long periods, covered with straw, in pits. Brockmann-Jerosch (1986) writing early this century recorded that acorns were still an important food in the Atlas Mountains, and that flour was ground in water-powered mills.

The process of acorn bread making in Sardinia has been recorded by numerous authors. Usai (1969) compiled many of the historical reports of acorn use in the Ogliastra district of eastern Sardinia, as well as observing the practice himself. The "bread" most commonly seems to have been produced by first boiling shelled acorns in water, then crushing them (a pestle and mortar, or piece of wood are mentioned), and adding red clay. Acorns might be crushed, or soaked in water, before boiling, and ashes might also be added. Boiling could take as long as eight hours. The resulting substance seems to have been rather similar to Californian acorn mush rather than a baked bread. It was described as "porridge" by Altheer (1857, cited in Gifford 1936), and was also compared with the chestnut "soup" of Tuscany. It was solid enough to cut into slices or form into "bread rolls", which might be wrapped in the leaves of citrus trees, or other aromatic plants, or powdered with ashes (see also Altheer 1857, cited in Gifford 1936). Occasionally the product was also baked in ovens, but this does not seem to have been common. It was usually dark brown or black, and was said to be similar in appearance to chocolate. It had a sweetish taste, though some writers also comment on an acidic taste or smell. It was eaten with lard, oil, pork, milk,

cheese, or honey. Acorns of both *Q. ilex* and "*Q. robur*" are mentioned, though the latter is not now recorded on the island.

Usai (1969) also recorded the process of production by one woman in 1957. Shelled acorns which had been dried in a bag hung near the chimney, were placed in a goat-skin bag, which was smashed against a stone in the kitchen until the acorns had split in two. They were then placed in a cauldron. Clay was dissolved in water in a separate terracotta pot. Two-thirds of this was poured into the cauldron, strained through a linen cloth to catch any grit. The cauldron was then placed on an iron tripod above the fire. As the cooking proceeded the mixture changed from red-brown to black. A small quantity of ashes were added. The cooking process continued for around five hours, occasionally topped up with the clay liquid. At this time acorn pieces which had not fallen apart were scooped out and placed in large rectangular wooden "baking tins". The remaining "porridge" was cooked further, then poured onto a table, where it was spread out and small round "cakes" were formed from the mixture. This product, known as "fitta", which Usai noted resembled soft chocolate, was considered a food for ill or delicate people, and eaten as a sweet by children. The solid material removed earlier, formed a substance like black nougat, called "lande", which was a "robust" food eaten by young men and those doing heavy work. Both were fairly compact substances. Any which was not going to be eaten within ten days or so was placed in cane chests, and hung up near the fire to prevent mould developing. Usai also reported one informant who remembered the making of flattened "pizzas" baked in the oven.

Parsons (1962, 214-215) noted that acorns were still used in the form of both gruel and bread in Spain, though they were more commonly sold in the markets "more as a confection than as a staple". Boiling was recorded as a method of preparation in North Africa (Howes 1948). Roasting, apparently usually of sweet acorns, seems to have been a common method of consumption on both the northern and southern borders of the Mediterranean (see, e.g., Gifford 1936). In Algeria and Morocco the "large acorns of a species of evergreen oak" were eaten both raw and roasted (Merriam 1918,136), and Loudon (1905, cited in Smith 1929) recorded that sweet acorns were eaten raw or roasted in these countries, and were regularly sold on the markets. In Spain sweet acorns were also eaten raw, as "sweetmeats" (Loudon 1907, cited in Smith 1929), and Clark (1986) records the roasting and eating of acorns as snacks in present-day northern Spain. Acorns were roasted and eaten with honey on Rhodes (Gifford 1936).

Al-Awam (Clément-Mullet 1977) described the preparation of stored sweet acorns in tenth century Spain, in a way which was said to make them as fresh as the day they were picked. Acorns were spread on moist ground and then covered with sand moistened with water.

Moistening was undertaken once a day for eight days. Acorns were then washed to rid them of sand, and eaten, apparently raw.

The use of acorns as a source of oil, comparable in quality with olive oil, has been recorded in Algeria and Morocco (Bainbridge 1985b; Loudon 1905, cited in Smith 1929).

3.2.6. Southwest Asia

3.2.6.1. Acorns in the subsistence system

Unlike the Mediterranean region, there do not appear to be many ancient documentary references to acorn eating in Southwest Asia, though Bainbridge (1985b) cites the inventories of the "belut" oak made in the Harran district of Assyria (now in southern Turkey) during the time of Sargon II (721-700 BC) suggesting they reflected the "vital importance" of acorns at the time. The precise reasons for which detailed records were kept is not apparently recorded, and Campbell Thompson (1949) considers that the galls (of *Q. infectoria*) which have been of great commercial importance in tanning, were the more likely reason. The use of acorns in the region in more recent times has been fairly frequently recorded, but often there is little detail available regarding methods of consumption. Acorns of "*Q. aegilops*", either *Q. brantii* (also often cited as *Q. persica*) or *Q. ithaburensis* ssp. *macrolepis*, are commonly cited as food, as is *Q. ilex* where it extends into the region (Campbell Thompson 1949; Gifford 1936; Hedrick 1972; Townsend and Guest 1980; Uphof 1968; D. Zohary pers. comm.). Irgens-Moller (1955, citing Schenck 1939) recorded that some of the acorns of *Q. robur* ssp. *robur* are sweet and edible and have been consequently been planted in "Asia Minor" (see also Burkill 1935; Hedrick 1972). Campbell Thompson (1949) mentions acorns of *Q. infectoria* as an "edible" species of Kurdistan, and notes that they were frequently brought into Mosul, in Iraq. Sachau (1883) noted the use of acorns in the Sinjar region of Iraq, and commented that he had seen this frequently on his travels.

Acorns have been reported to have been a major element in the diet of both nomadic pastoralists and settled agriculturalists through the Zagros Mountains of western Iran (see, e.g., Amanolahi-Baharvand 1975; Bird 1891; Casimir 1988; Hole 1978, 1979; Watson 1979), and are suggested to have been a staple food there in the late nineteenth century (Bainbridge 1985b). They were also widely used in Arabia and Palestine during the same period (Bainbridge 1985b). Fieldwork carried out in Southeast Turkey in 1990 demonstrated that this may also have been the case in parts of that region. Acorns were sold in markets in nineteenth century Palestine (Hedrick 1972), and throughout the region until

recently (Bainbridge 1985b). They have been sold in Turkish markets within the last couple of decades (G. Hillman, F. McLaren pers. comm.).

Acorns have also been recorded as fodder for livestock in Iraq (Townsend and Guest 1980), and Hole (pers. comm.) noted that they were sometimes collected for feeding to livestock in western Iran. Acorns are an important food for cattle and goats in Israel, and are also sometimes collected for stall-feeding, possibly of horses (D. Zohary pers. comm.) Collection of acorns by hand for feeding to goats has also been seen by the author in southeast Turkey (see 3.2.6.3.).

Though acorns are often referred to as more commonly eaten during times of hardship, the available data indicate that they had a wider-ranging importance, and in many cases were the principal plant food, even amongst those practising agriculture. Bird (1891) travelling in Bakhtiari country, Luristan, in western Iran recorded the use of acorns. Some groups, who had recently begun to grow crops, lived on the products of their animals, wheat and barley bread, and a paste made of acorn flour. Another group, who apparently spent four months of the winter snowed up in the mountains also owned animals and grew wheat, but sold this, and lived on acorn bread, curds, and wild celery. Wilson (1932 cited in Gifford 1936) described acorns in this area as a "supplement" to the "meagre store of cereals", but also reported families who survived only on acorn bread and the produce of their herds, and commented that they were in good physical condition. Hole's (1978) study of the Baharvand, Luri-speaking people from western Iran, found that though now much of subsistence derives from agriculture, this was not always the case. Atawak, an 85-year-old informant, had previously subsisted entirely independently of agriculture, relying mostly on acorns and wild grains, hunted meat, and the products of herds and trading. Resort to acorns was now carried out only in times of economic stress. Amanolahi-Baharvand (1975) working with the same people, thought that, if necessary, they could subsist on acorns without doing farming, and with a minimum of dependence on their domestic animals.

3.2.6.2. The harvesting/processing sequence

3.2.6.2.1. Harvest and storage

Bird (1891) recorded that acorns were not picked, but gathered when they fell, while Hole (pers. comm.) reported that acorns were collected in the autumn by beating the trees. Acorns could be collected almost to the end of winter, and they could be used anytime they were found. Watson (1979), slightly further to the north, reported that January was considered late to find acorns. She also noted that acorns collected before the first rains

were considered to be bitter. Acorns were dried in the sun, and she reports information obtained from Bakhtiari country in southwestern Iran where large numbers of acorns were noted drying on the roofs.

The extent to which storage, or transport, of acorns was undertaken in western Iran is unclear. Pastoralists movements involved leaving the mountainous regions where oaks occur for the winter, and only returning in the spring (Bird 1891; Hole 1978, 1979). Hole reported bulk processing facilities (described below) found near oaks in the mountains, and noted that campsites were not usually to be found in the vicinity, suggesting that processed acorns may have been transported. He also described storage bins used now for cereals, either above-ground and made of mud, or pits in the ground lined with straw-tempered mud, and suggested these may have previously been used for acorns.

3.2.6.2.2. Food preparation

Acorns seem most commonly to have been made into flour, from which preparations such as bread or "paste" were subsequently made (Amanolahi-Baharvand 1975; Bird 1891; Casimir 1988; Hole 1978; Townsend and Guest 1980; Watson 1979).

Bird (1891) reported that acorns were first bruised between two stones to expel bitter juices. They were then made into flour, and washed in water to remove any remaining bitterness. The flour was then dried in the sun. It was made into thin cakes and baked, or mixed into a paste with buttermilk and water and eaten raw. Wilson (1932, cited in Gifford 1936) recorded that acorns were pounded to a pulp with a boulder rolled over a flat rock. The meal was then soaked in running water for several days, dried and then made into flat cakes, which was said to keep well. Stark (1934, cited in Watson 1979) also recorded that acorns were first soaked in water before being made into flour. Sachau (1883) recorded that acorns were processed in the Sinjar region of Iraq, by first boiling in water to asist in removing the shells. The acorns were then crushed into flour paste and baked into bread.

Hole (1978) reported the method of bulk processing used by the Baharvand, in western Iran. This first involved roasting on roofless rectangular stone structures 1.5m^3 in size. Nearby acorn "smashers", consisting of a large rock on which another sat, were used to grind the acorns. He recorded one so large that the upper stone could not be picked up and was just rocked back and forth over the acorns. Hole (1979) also noted that mortars and pestles were used, apparently for both cereal and acorn processing, and bedrock mortars, often consisting of a line of several depressions, were used for producing acorn flour. He also noted the presence in the region, dating back to c. 200 B.C., of water-powered mills, now used for processing grain. Since some informants reported that they did not grow

cereals in the past, it is possible that they may have been used for acorns, though this is not clear. Watson (1979) reported the use of rotary querns to produce acorn flour.

Amanolahi-Baharvand (1975) recorded that the Baharvand made two kinds of bread from acorns, both of which took almost two weeks to prepare. One was made from acorns only, and another, which was preferred was a mixture of acorn and wheat flour. Hole (pers. comm.) has recorded the method of preparation in more detail. Acorns were shelled, and roasted in an oven. They were then put in water for 20-30 days, dried, and then smashed. Hot water might then be poured over the smashed acorns, and they were then cooked as flour. More detailed information was provided by an older woman, who said that shelled acorns could be roasted or fried in pans, and were then dried completely in the sun. The testas were then taken off, and acorns were smashed on a stone. Boiling water was poured twice through the smashed acorns, and they were then left to soak for a day in a skin bag until they were soft, and could be mashed with the fingers. The acorn mixture was placed in a basket with leaves on the top and bottom, where they were left for three days to ferment, and were then placed in a waterfall overnight. Bread was made in several ways. The paste could be further ground, put in a cloth and then flipped onto a breadpan. A mixture of acorn and wheat paste might be used to make thin bread in the same way. Another thicker form was made with the addition of more acorn flour. Acorn paste could also simply be mixed with yoghurt and eaten. Another food was made fom shelled fried acorns placed in bags in a stream for a week. These were taken to a mill to make flour, and then bread was made using one part acorn flour to two parts wheat flour.

Acorns are also recorded to have been eaten after roasting in the ashes, in their shells. Shells were sometimes first split to allow steam and bitterness to escape. Unsplit acorns would be cooked when they popped, and they would be shelled and eaten (Hole pers. comm., Watson 1979). The acorns of *Q. libani* were eaten roasted in Iraq (Townsend and Guest 1980). Acorns are recorded to have been eaten "cooked" in nineteenth century Arabia, and oil was also extracted from them (Hedrick 1972). Howes (1948) describes a "popular dish" called "racahout" made in Turkey. Acorns were buried in the earth after collection, then ground, washed and dried and sugar and spices added.

3.2.6.3. Acorn use in Southeast Turkey

Fieldwork undertaken in Southeast Turkey in October 1990 produced considerable information about past and present human consumption of acorns, in an area where it has apparently previously remained unrecorded (Mason 1991). Information was obtained from the region of the Tur Abdin, a limestone plateau lying southeast of Diyarbakir and stretching south to the Syrian border, and from the foothills of the Nemrut Dagı mountain

range, west of the Firat (Euphrates) and south of Malatya. Two species were used - *Q. brantii*, which dominates the Tur Abdin, and is relatively sweet, and *Q. infectoria* ssp. *boissieri*, which occurs in more or less equal numbers with *Q. brantii* in the Nemrut area, and has more bitter acorns. *Q. brantii* appears to have been a more favoured food, but both could be used. Nutritional analyses of some of the collected acorns are included in Table 8. Older trees and those growing in valleys were said to yield best, and though total crops vary from year to year there were "always enough" acorns. Certain trees consistently yield larger crops or sweeter acorns and these were protected in the past. It was possible to improve yield by pruning trees, for example by removing side branches and leaving a major central one. Two years after cutting a tree will produce fewer, but bigger and better acorns.

All informants said that, though bread was no longer prepared from acorns, this had been done until perhaps 40 years ago, and they had been used as such during the last war. Few details of the process of bread-making were obtained, but acorns were ground with hand rotary querns, similar to those used for grinding of grain today. Acorn flour would sometimes be mixed with barley flour before baking.

The main use of acorns now is as a snack food, but they are still apparently gathered in considerable quantities and stored for this use. Acorns are best collected after they have ripened and fallen to the ground. Acorns were still on the trees that year in mid-October, and informants suggested the best time to harvest would be in about a month. Acorns are inspected for insect or other damage, sometimes by placing in water, when the bad ones float. They may be boiled to kill any insect larvae. Acorns are dried in the sun, sometimes on rooftops. If left to dry for a month or so they will lose any bitterness and will have become hard enough to grind into flour. Some acorns may be stored in pits dug in the ground, or in 20 litre tins where they may be placed in layers separated by soil. They will keep for two or three months at least, though after four months they may begin to germinate. Any remaining bitterness disappears with time. Storage seems to have taken place with acorns still in their shells.

Freshly-collected acorns could be used immediately by having their bitterness removed by boiling. Shells split on boiling or drying and can be easily removed with the fingers. Acorns may be lightly roasted, which helps in the removal of shells and the bitter testa. The kernels are sometimes eaten wrapped in pestil, a rubbery paste made from pulped fruits of various kinds, dried into a solid sheet and then cut into strips. An alternative use of acorns is to roast them fully, grind them, and make into a "coffee" which is said to be better than the real thing.

Q. brantii was also recorded eaten raw. The 'proper' way to peel and eat a raw acorn was demonstrated by one informant. The cupule was removed with a knife, and the base of the acorn shell, including the abscission scar, sliced off. The remainder of the shell was peeled off with the knife in longitudinal strips from the base, and the testa was scraped off, again with the knife. Sections of the acorn were then cut off and eaten, until the tip was reached. This was discarded because it tastes more bitter. Water tastes sweet when it is drunk after eating raw acorns. Encounters with two elderly women, one in each area, provided further evidence. One was carrying acorns in her pockets, and both eagerly demonstrated the eating of acorns and insisted what excellent food they were; though not all informants were equally keen.

Acorns are also important fodder for goats in the area. A harvesting party of young women and boys on the Tur Abdin were observed picking acorns from abundantly-fruiting 2m-high coppice shoots, currently managed principally for fuel. The cupules were bitten off and discarded as the acorns were picked, and the still-green acorns were placed in carrying bags. According to one informant feeding of acorns to goats improves their milk. They are fed whole or broken up with a hammer.

3.2.7. Mainland Eastern Asia

There are reports of the use of acorns for human food from this region, but few details are available. Uphof (1968) reported that acorns of *Q. glauca* was eaten in parts of Himalayan India, and Tanaka (1976) recorded that acorns of *Q. semecarpifolia* were roasted there (see also Bainbridge 1985a). Their most important use in India in recent times seems to have been as animal fodder, though some work has also been undertaken on the potential for extraction of oil from acorns for industrial use and human consumption (Gul and Khan 1982; Puntambekar and Varma 1934). Watt (1889-1896) did not record any use of acorns for human food in India, though acorns of several species were used, and sold on markets, as medicine. He recorded that acorns were first buried in the earth to remove their bitterness, then washed and ground, before administering.

Morris (1927) recorded the use of six species as food in Thailand, most of which were sweet and were eaten roasted, and Tanaka (1976) reports edible acorns in Burma. Burkill reported that edible species of "acorn" were known in Malaya, though these include nuts of the genus *Lithocarpus*. Hedrick (1972) reported that acorns of several species of oak were eaten in nineteenth-century China, and that a kind of curd was made from the ground flour. Simoons (1991) reported several historical references to the use of "edible" acorns in China (see also Tanaka 1976), and noted that they continue to be used as food and medicine.

Bainbridge (1985a) also reports several species recorded as food in China, and notes that some are still sold on the markets (1987).

Acorns are eaten in Korea, where between 1.0 and 2.5 million litres are commercially harvested a year. A preparation called "mook" is available even in Korean delicatessens in the United States, and acorn flour imported from Korea is also sold there (Bainbridge 1985a, pers. comm.). Though no details are available regarding the traditional processing of acorns, the "mook" is "jelly-like" and its description resembles that of acorn mush prepared in California. Acorn flour is also incorporated with other flours and used in the preparation of noodles (Sung-Mo Ahn pers. comm.).

3.2.8. Japan

3.2.8.1. Acorns in the subsistence system

In mountainous regions of Japan wild food resources were often of great importance amongst people practising subsistence agriculture until the nineteenth century, and sometimes later (see, e.g., Koyama 1978, 1981; Matsuyama 1981). Koyama (1981) recorded that nuts were the most important of these resources in the Hida area, though wild roots were also very imortant. Koyama (1981) commented that through Japan as a whole chestnuts (*Castanea*), buckeye (*Aesculus*), acorns, walnut (*Juglans*), hazelnut (*Corylus*) and Japanese nutmeg (*Torreya*) were most commonly used, and the first three were most important. Matsuyama calculated that at the end of the nineteenth century here nut products, including acorns, accounted for 20% of staple foodstuffs. Gathering of acorns and buckeyes (*Aesculus turbinata*) was combined with cultivation of upland and paddy rice, and together with millet these all seem to have been staple foodstuffs. Though the contribution to the diet of acorns is not reported separately, both deciduous and evergreen acorns were widely utilized as "important food resources" (Matsuyama 1981,133). The importance of acorns in Japanese diet is also indicated by the reported use of between eight to ten species (out of a total of around fourteen) summarised by Bainbridge (1985a) and Tanaka (1976).

3.2.8.2. The harvesting/processing sequence

Matsuyama (1981) summarised the ethnographic data from early this century on acorn processing, together with data on buckeyes, from a total of 43 Japanese villages, and it is from this account that the most of the following information is taken.

3.2.8.2.1. Harvesting

The harvesting of acorns was not reported in detail, but Matsuyama described the harvest of buckeyes, which took place on a day decided by a few elders, and could be done communally, especially when resources were particularly rich or particularly poor, or individually. They were apparently collected mainly when fallen, though trees might be shaken to bring down more buckeyes. Acorns were collected in baskets attached to the gatherer's waist, and then emptied into hemp sacks.

3.2.8.2.2. Storage

Acorns were sometimes dried, in sun or shade, before processing, and though buckeyes might also be hung above a hearth to complete the process prior to storage, this was not recorded for acorns. Storage of whole acorns was not commented on, though buckeye nuts would keep for several years provided they were aired once a year. Matsuyama (1981) did record the storage of acorn flour was stored, but no details were given. According to Kidder (1968, 24) it is "possible to preserve acorns for at least a century using boiling and drying techniques known today", but what this statement is based on is not clear.

3.2.8.2.3. Food preparation

3.2.8.2.3.1. Shelling

Various tools were used for shelling nuts, including natural or slightly modified stones, the teeth, or stone or wooden hammers or mallets. Nut crackers consisting of two hinged pieces of wood are pictured by Matsuyama (1981, 128, fig. 5), though he only discusses these in relation to buckeye shelling. Though in some cases Matsuyama records that great care was taken not to damage the kernels in shelling, in others it seems to have been accomplished by smashing the whole nut, shell and all, with a pestle and mortar or on a concrete floor, pounding, and then winnowing to get rid of the shell. Shelled nuts could also be broken into smaller pieces by hammering on a flat stone, using a mortar and pestle, or water mills. Koyama (1978) reported that milling slabs and handstones were used for producing acorn flour.

3.2.8.2.3.2. Leaching

Leaching of acorns was a necessary step in the production of acorn "cakes". This was achieved by a combination of water-leaching, addition of lye, and leaching in boiling water, with the simpler water-leaching apparently used for the sweeter evergreen oak acorns.

Though he also comments that tannins are more readily leached when acorns have been finely ground this process was recorded in all three cases of processing of evergreen acorns, but only in one of six of deciduous acorns. Deciduous acorns were usually reduced to fine flour by the prolonged soaking and boiling used in their preparation. The use of lye was only recorded in the processing of deciduous oak acorns. Matsuyama reoported the method of preparation of lye for buckeye processing. Into a bucket with small holes in the bottom was placed a layer of rice bran. Ashes were placed in the bucket, equal in quantity to the amount of buckeye to be processed. Hot water was poured slowly into the bucket and the lye oozed out of the holes. Lye produced with water that was too hot was thought to be bad, as it turned the buckeye pieces red. Though wood ashes were used in this case, he also commented that the ash made from the stems of buckwheat (*Fagopyrum*) were the preferred material in the production of lye for buckeye processing.

Water-leaching was achieved in several ways. Flour was placed in a receptacle such as a hemp sack, or in a bag inside a basket, to prevent it being washed away. It could then be soaked in a stream or placed under falling water for seven days to a month (see also Koyama 1978), perhaps being stirred by hand occasionally to facilitate tannin removal. Sometimes flour was just placed in a pail and water continuously dripped in, with the whole stirred occasionally; or the flour might be mixed with plenty of water and allowed to settle, after which the water was poured off and the process repeated several times.

In the case of deciduous acorns this water-leaching would often be followed by a boiling process to further remove tannins. In some places boiling would precede or replace water leaching. In one case whole acorns were boiled complete with shells on, then dried and shelled before being processed by further leaching. Acorns might be simply boiled in a container, or a more elaborate technique might be used. In one village, for example, the flour was placed in a large pot with a cylindrical drain-basket placed in the centre. The mixture was boiled slowly for at least 24 hours, with water added about twelve times, as the water containing leached-out tannins was scooped from the central drain-basket.

3.2.8.2.3.3. Cooking

Once processed, acorn flour could be used immediately, or it might be drained and dried, and then stored. As a preliminary stage of cooking, the leached acorn flour was usually soaked in hot water for a while to produce a sticky dough. Sometimes the flour was used on its own, or it might be mixed with rice flour or soybean flour. The dough cakes could then be eaten, sometimes first baked or steamed.

Matsuyama described the preparation of "gruel" from buckeyes, but this was not specifically mentioned for acorns. Tanaka (1976) however recorded the use of acorn flour of several species to make "gruel". The most common use of acorn flour which he reports is as "dumplings", which may be the same as the "cakes" described by Matsuyama (1981). He also recorded acorns as a source of edible starch. Other species were eaten whole after soaking in water to remove bitterness. Gifford (1936) quotes a report of the eating of boiled acorns, though it is not certain whether this was simple boiling, or whether it was a leaching process such as described above. Morris (1927) reports that acorns of *Q. glauca* were eaten "cooked".

The roasting of less bitter acorns has also been reported (Koyama 1978; Uphof 1968) though in some cases this refers to "acorns" of *Castanopsis* and *Lithocarpus*. Tanaka (1976) also recorded the use of acorns roasted as coffee substitutes.

CHAPTER 4. TAXONOMY, DISTRIBUTION AND ECOLOGY OF OAKS

4.1. INTRODUCTION

The oaks (*Quercus* spp.), comprise the largest genus of the Fagaceae, an important family of evergreen or deciduous trees (occasionally shrubs) of temperate and tropical areas. Because of its large size and wide distribution there have been few overviews of the genus as a whole. The most recent monograph on the oaks is that of Camus (1936-1954), and there have been overviews of the species of Europe (Schwarz 1936-1937), America (Trelease 1924), Asia (Menitskii 1984), Malesia (Soepadmo 1972), Central America (Muller 1942a) and parts of Southwest Asia (Zohary 1961; Browicz 1982; Djavanchir-Khoie 1967; Hedge and Yaltirik 1982; Townsend 1980).

All members of the Fagaceae produce what are botanically-speaking nuts, all of which are potentially edible. The acorn, defined here as a single nut surrounded at the base by a tightly-fitting cupule, is characteristic of all species of *Quercus*, but is also found in the genus *Lithocarpus*.

4.2. ORIGINS AND FOSSIL HISTORY

The Fagaceae are thought to have originated in the montane tropics, with *Quercus* itself probably originating in what is now Southeast Asia, where the least specialised members of the genus are found (Kaul 1985). Several features of the biology of *Quercus* support this hypothesis. The possession of a very short flushing period, followed by recurrent flushes (e.g., the "Lammas shoots" of British oaks) is characteristic of species of the tropics and sub-tropics (Longman and Coutts 1974). Pollination takes place early in the year in both temperate and tropical species, a reflection of the likely evolution of the genus in seasonal parts of the tropics (Kaul 1985). Large seed size and recalcitrance, both characteristic of *Quercus*, are thought to be features related to survival in moist sub-tropical or tropical forest habitat (von Teichman and van Wyk 1991). The family spread as part of the expansion of the angiosperms, and diverged into most of the living genera by the later Cretaceous. *Quercus* underwent rapid evolution from the mid-Tertiary onward, proliferating particularly in certain restricted areas of mild- to warm-temperate climate at times when topographic, climatic and edaphic diversity was increasing - particularly in Mexico/Central America, the Southwestern United States, the Mediterranean basin, and Southeast Asia. The rise to dominance of oaks is thought to have occurred in temperate forests through selection for greater drought- and high temperature-resistance in areas such as California, Arizona, Spain and Turkey, and for cold resistance in continental interiors of

northeastern Asia and the central United States; and in tropical montane regions by radiation, as Tertiary uplift occurred (Axelrod 1983).

4.3. TAXONOMY

Classification of *Quercus* is complex, and there have been frequent revisions both of its relations within the Fagaceae and within the genus itself at all levels.

4.3.1. The Fagaceae

SUBFAMILY	GENUS
Fagoideae	Fagus Nothofagus
Castaneoideae	Lithocarpus Castanopsis Castanea Chrysolepis
Quercoideae	Trigonobalanus Quercus

Scheme proposed by Forman (1964).

SUBFAMILY	GENUS
Fagoideae	Fagus
Castaneoideae	Lithocarpus Castanopsis Castanea Chrysolepis
Trigonobalanoideae	Trigonobalanus
Quercoideae	Quercus

Scheme proposed by Jones (1986). Nothofagus is now separated in Nothofagaceae.

SUBFAMILY	GENUS
Fagoideae	Fagus Trigonobalanus Colombobalanus Formanodendron Quercus
Castaneoideae	Lithocarpus Castanopsis Castanea Chrysolepis

Scheme proposed by Crepet and Nixon (1989).

Table 1. The relationship of *Quercus* to other genera of the Fagaceae

All members of the Fagaceae are characterised by a fruiting structure composed of single-seeded nuts, in groups of 1-3, subtended by a cupule, formed of several bract-like structures, fused to varying degrees depending on genus - a feature unique to the family (Heywood 1978). The family has been variously sub-divided, with the system of Forman (1964), for long the standard, recently re-assessed by Jones (1986), Nixon and Crepet

(1985, 1989), and Nixon (1989). It is unlikely that the situation will remain unchanged, as investigations into the taxonomy of the family are far from complete (see, e.g., Corner 1990).

4.3.2. The genus *Quercus*

Quercus is distinguished from other members of the Fagaceae by the presence of solitary pistillate flowers, in unisexual spikes, and by the nature of the cupule. Classification within the genus has presented difficulties so that some have classified others' subgenera as genera, or as sections, and even the concept of the genus itself has caused controversy amongst taxonomists (see, e.g., Irgens-Moller 1955). Some have suggested that *Cyclobalanopsis* should be treated as a separate genus, and others that *Lithocarpus* should be included within *Quercus* (Jones 1986). The cupule of *Cyclobalanopsis* is lamellate, a feature found also in some members of *Lithocarpus*, which also contains members with scaly cupules, as are found in *Quercus* (Kaul 1985).

SUB-GENUS	SECTION
Cyclobalanopsis	
Quercus	Cerris Mesobalanus Lepidobalanus Macrobalanus Protobalanus Erythrobalanus

Modified Camus system

SUB-GENUS	SECTION
Cyclobalanopsis	
Quercus	Rubrae (= Erythrobalanus) Protobalanus Cerris (includes some previously included in Quercus) Quercus (= Lepidobalanus)

Nixon and Crepet (1985)

SUB-GENUS	SECTION
Cyclobalanopsis	
Quercus	Rubrae Protobalanus Ilex Leucobalanus

Crepet (1989)

Table 2. Subdivisions of *Quercus*: modified Camus system and recent revisions

Subdivision of the genus has usually followed the system proposed by Camus (1936-1954). Of recent revisions of oak taxonomy this system was accepted by Jones (1986), but Nixon and Crepet (1985) and Crepet (1989) have proposed alternatives, shown in Table 2.

4.3.3. Nomenclature

There is no nomenclatural system for *Quercus* below the level of sub-genus generally accepted for all areas where members of the genus are found. Here, the division between *Cyclobalanopsis* and *Quercus* will be treated, as by Camus, as sub-generic, while other taxonomic divisions will be referred to as "groups" in preference to section or sub-section. In discussions of North America the terms "red oaks" and "white oaks" have been used for the *Erythrobalanus* and *Lepidobalanus* groups. For species names and groupings in particular regions the following sources have been used: North America - Miller and Lamb (1985), Europe - Tutin *et al.* (1964), except for those species which also occur in Turkey - Hedge and Yaltirik (1982), Japan and adjacent areas - Ohwi (1965). Otherwise, reference has been made to Camus (1936-1954) and Index Kewensis (1946-1991).

4.3.4. Classification and variability of species

Classification and nomenclature has been particularly confusing at both inter- and intra-specific levels because of the great morphological variability of oaks. Species have often been divided into numerous sub-species, varieties and forms which some argue may be taxonomically doubtful, as they merely reflect phenotypic plasticity (e.g., Irgens-Moller 1955). Because of these difficulties the number of species of *Quercus* has been estimated by different authorities at anything from 300 (Elias 1971; Lawrence 1951) to 600 (e.g., Soepadmo 1972).

4.3.4.1. Hybridisation

There are apparently frequent occurences of hybrids in *Quercus* (see, e.g., Burger 1975; Cousens 1963; Guttman and Weigt 1989; Irgens-Moller 1955; Muller 1941; Stebbins *et al.* 1947; Tucker 1980) usually between species within sub-generic taxonomic groups. Hybridity generally tends to occur between allopatric species in zones of range overlap, and hybridization between sympatric species is probably less common (Irgens-Moller 1955 - cf. also Sauer 1990). According to Tucker, F1 hybrids are often fertile, and produce large numbers of viable acorns. However, the level of hybridization in oaks has been difficult to assess since most studies have been based on examination of morphological characters, which are notoriously variable in oaks, and thus may not be reliable discriminants of either species or hybrids (e.g., Brookes and Wigston 1979). Thus Muller (1952) claimed that hybridization is not as common as it appears, since most claims are made on the basis of variation in trivial characters which can be found within a pure population of a single species. Others have noted that the frequency of hybrid trees within populations of parents

is often low (Irgens-Moller 1955; Jones 1959), and hybrid swarms are relatively rare partly because of lack of suitable habitat (Irgens-Moller 1955).

Other studies have used measures of pollen viability as indicators of hybridity (e.g., Minihan and Rushton 1984; Rushton 1978, 1979); and variability in leaf trichome characters (Hardin 1979) and phytochemistry has also been examined (Cristofolini 1985; Fairbrothers *et al.* 1985; Guttman *et al.* 1985; Hunt 1985) as an aid to studies of hybridity and other taxonomic investigations.

4.3.4.2. Introgression

Partly because of the difficulties alluded to above there has been much debate about the occurrence and extent of introgressive hybridization within *Quercus* (see e.g., Wigston 1974). In cases where introgression has been demonstrated it may sometimes be associated with disturbance of the habitat (Irgens-Moller1955; Minihan and Rushton 1984) or with human planting of trees (Ietswaart and Feij 1989).

4.3.4.3. Variation and phenotypic plasticity

The oaks demonstrate great inter- and intra-specific variation. There is wide variation between species in growth habit, in ecological preference, in altitudinal distribution, and in reproductive strategy, as well as in morphological characters, anatomy, physiology and biochemistry (Irgens-Moller1955; Jensen 1985). The extent of variability and overlapping characters is such that some have even questioned whether the biological species concept can be applied within the genus (Burger 1975; Muller 1942b; Trelease 1924; Van Valen 1976). To what extent this variation is a result of hybridization and introgression is a matter for debate, and arguments are complicated by the fact that both phenotypic variation and hybridization are influenced by environmental factors (Anderson 1948; Muller 1952; Rushton 1979). Great plasticity is apparent in similarity of leaf form and acorn type, for example, even among species belonging to different sections which have undergone long periods of separation and adaptive radiation (Axelrod 1983; Jones 1986); and Cristofolini (1985) suggests, on the basis of biochemical studies, that phenotypic plasticity may be a more likely cause of morphological variability than inter-specific hybridization or introgression. Hardin (1979), using leaf trichome characters, concluded that hybridization and introgression within the oaks tended to be localized, and though fairly frequent, accounted for less inter-specific variability than there was intrinsic variation within an individual species. Wide geographical distributions (and therefore phenotypic/ecotypic differences) may account in part for the large variation in leaf shape and form within some species, while the intergradation of foliar variation between species might be partly the

result of gene flow between them caused by introgression (Jones 1986). Studies of pollen morphology and biochemistry carried out on North American oaks have suggested a greater and/or more recent amount of variability in the red oaks than in the white oaks, perhaps occurring through greater hybridisation and introgression (Guttman and Weigt 1989; Solomon 1983a, 1983b).

Some of the variability present in oaks may be a direct reflection of genetic variation, related to the nature of the breeding system (see Wigston 1974), or to high levels of heterozygosity resulting from ancient crosses (see Irgens-Moller 1955). Environmental factors may also produce some of the observed variability, including modifications due to ecological stress, or as a result of stump-sprouting (Irgens-Moller 1955).

4.3.4.4. Evolution

The role played by inter-specific hybridization and introgression in gene exchange, speciation, and evolution within the oaks is also cause for some debate, and is particularly difficult to assess because of the long timespan between generations (Stebbins *et al.* 1947). Because intra-specific variation is great it tends to fill intermediate niches which might be occupied by new species or forms. Specific distinctions may be maintained by ecological factors (Muller 1952), as well as by those biological factors that restrict gene flow (Stebbins *et al.* 1947). Nevertheless, many believe that introgression must have played some part, and the capacity for gene exchange may be one of the factors that makes the oaks very competitive in a wide range of environments (Van Valen 1976).

4.3.4.5. Vegetative reproduction

Many oaks are capable of sprouting vigorously from root-crowns, stumps or within the canopy when cut, burnt or browsed, and many present stands of oak have originated in this way rather than directly from seedling growth (see 4.6). Most species do not reproduce vegetatively other than in this manner, with the exception of some shrub oaks. *Q. sadleriana* of Northern California and Oregon regenerates from "rhizomes", or by rooting at the nodes (Muth 1980). *Q. chrysolepis* var. *vaccinifolia* can spread by "layering", or rooting from its branches (Biswell 1974). *Q. pumila* and *Q. prinoides* are described as stoloniferous shrubs, while the Mexican *Q. depressipes*, is said to form thickets via underground stolons (Miller and Lamb 1985).

Investigations by silviculturists have shown that some oaks at least can be vegetatively propagated, either by rooting basal cuttings from young trees, or by grafting (Irgens-Moller

1955). Grafting with high acorn-yielding individuals of *Q. ilex* has been used extensively in Iberia in the dehesa/montado pig-fattening systems (Parsons 1962).

4.4. DISTRIBUTION

Quercus is the largest and most widely-distributed genus in the Fagaceae, occurring throughout temperate and subtropical areas of North America and Eurasia, with an extension into North Africa, and into the montane tropics of Central and northern South America, and Southeastern Asia as far as the Malesian islands. The oaks are frequently dominants of the northern temperate forests and woodlands, as well as of montane forest in the tropics.

SUBFAMILY	GENUS	DISTRIBUTION
Fagoideae	Fagus	North Temperate
	Trigonobalanus	Southeast Asia
	Colombobalanus	South America
	Formanodendron	Southeast Asia
	Quercus	See sectional distribution.
Castaneoideae	Lithocarpus	E & SE Asia, N America
	Castanopsis	E & SE Asia
	Castanea	North Temperate
	Chrysolepis	W. N. America

Scheme proposed by Crepet & Nixon (1989). Distributions from Hickey & King (1981) and Jones (1986)

Table 3. Distribution of the genera of the Fagaceae

Their main area of distribution is in warm-temperate to tropical montane areas. Although one or two *Quercus* species may occur as far north as 60°N, most reach their northern limit by 50°N at the most, and the genus mostly occupies latitudes equatorward of 40°N, with the highest concentrations in latitudes 15°-30°N in Mexico/Central America (with *c.*200 species) and Southeast Asia and the adjacent islands (*c.*130 of *c.*175 Old World species), particularly in southeastern China (Jones 1974). The principal ecological control over distribution of the genus is probably daylength, with 80% of species occurring in areas with less than 14 hours maximum daylength (Axelrod 1983).

The modern centres of morphological diversity (in both the Fagaceae and *Quercus*) are in Southeast Asia and adjacent islands, and in Mexico.

4.4.1. Distribution of the subgeneric groups

The *Cyclobalanopsis* sub-genus, (with *c.* 100 species) is restricted to Southeast Asia and the adjoining islands, in the latter of which it occurs without *Quercus*, while the sub-genus *Quercus* is found throughout the area of distribution of the genus, with the exception of this latter area (Kaul 1985).

SUB-GENUS	SECTION	DISTRIBUTION
Cyclobalanopsis		Southeast Asia
Quercus	Cerris	Europe, Asia
	Mesobalanus	Europe, Asia
	Lepidobalanus	Europe, Asia, North Africa, North America
	Macrobalanus	American tropics
	Protobalanus	American subtropics
	Erythrobalanus	North and Central America

Table 4. Distribution of *Quercus*: sub-generic groups

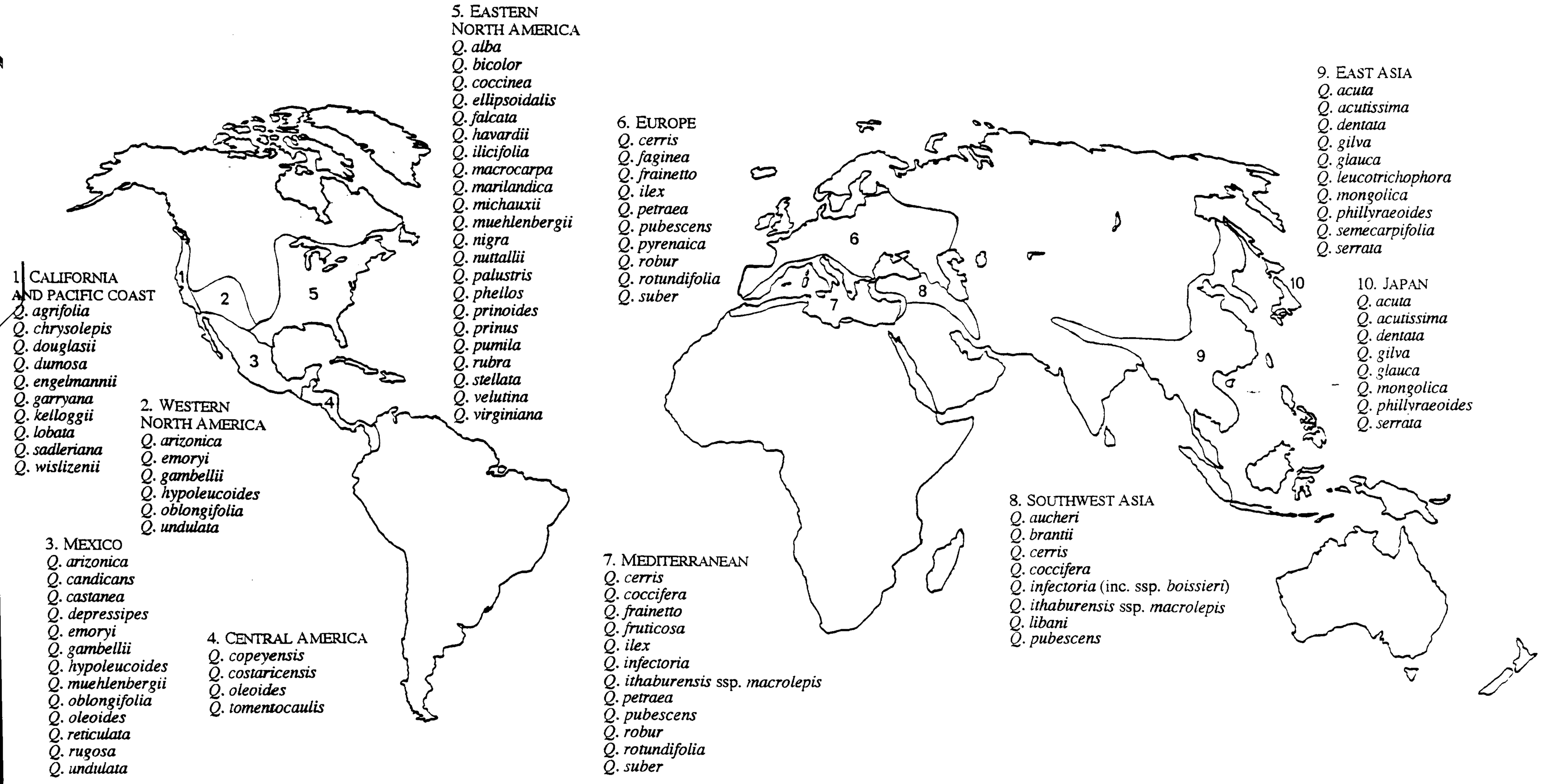
4.4.2. Species distributions

As discussed in 4.2, many features of the biology of oaks indicate their origin in warm temperate or tropical areas (Jones 1974), but they have subsequently undergone adaptive radiation into a wide range of climatic and ecologic zones. There is wide variation between species in ecological preference, from xeric to riparian habitats and from closed-canopy forest to open savanna-like or chaparral habitat; in altitudinal distribution, from sea level to *c*.4000m (in the Himalaya); and in the responses to these, such as growth habit and reproductive strategy. The distribution of oaks within various environments is discussed in greater detail in the following section, and the general areas of distribution of species mentioned throughout the text is shown in the map overleaf.

Distribution maps of individual species in various parts of the world can be found in the following references: Asia - Menitskii 1984; Southwest Asia - Browicz 1982; Zohary 1973; Turkey - Hedge and Yaltirik 1982; Europe - Jalas and Suominen 1976; Japan - Japanese Forest Technical Association 1964; America - Preston 1961; Miller and Lamb 1985; Little 1971-1981.

4.4.3. Phytogeography of oaks

Despite their acknowledged importance in many of the ecosystems in which they occur there is no worldwide overview of the role of oaks within vegetation types. The history of the spread and adaptation of oaks into different environments, through the Tertiary and beyond, has, however, been summarised by Axelrod (1983), who points out the great range of environmental conditions in which the genus is found. These vary from the montane tropics, with a twelve-month growing season, to the edges of the boreal zone, where the growing season may be as short as three months; and from the humid tropics and temperate forests to the borders of deserts and areas with very irregular precipitation. The great range of environments occupied by oaks is reflected in their adaptations. For example, species in the montane tropics are predominantly evergreen, while those found in



Map showing generalised regional distribution of *Quercus*, giving species mentioned in the text

northern temperate latitudes are deciduous. Axelrod also comments on the similarity ofecological position occupied by many taxa in the temperate, mixed-deciduous forests of North America, Europe, and Eastern Asia, and it seems that the oaks comply with this pattern, and are frequently dominant species throughout these regions. Similarities in the ecology of oaks between different regions occur in other vegetation types, notably the montane forests of sub-tropical and tropical zones in central America and southeast Asia, and the broad-sclerophyll vegetation characteristic of mediterranean-type ecosystems both in the Mediterranean and in western North America, all of which are described further below.

4.4.3.1. Oak distribution by vegetation type

The major vegetational groupings and climatic and geographical regions in which oaks are found are first briefly summarised, travelling roughly from high latitudes equatorwards.

4.4.3.1.1. Broadleaved deciduous forest

Oaks are found through much of the broadleaved deciduous forest of the Northern Hemisphere, generally within the temperate zone. In North America they occur throughout this vegetation type in the east, while in the west they occur predominantly in California. In Eurasia they are found throughout the broadleaved deciduous forest of Europe, extending to the borders of Asia in two arms: in the north to the Urals, and in the south through the Balkans to Turkey and along the Zagros Mountains into southwestern Iran where they form the southernmost spur of deciduous forest in western Asia. Eastwards, deciduous oaks reappear to the north in the deciduous forests of eastern Siberia, and to the south in the temperate zones of China, Korea and Japan.

4.4.3.1.2. Broadleaved evergreen forests

In the Americas oaks occur as components of this vegetation type in California and the Southeast, and in montane zones within the tropics and sub-tropics. In Europe and southwestern Asia they form a transition between the mesic deciduous forests and the drier maquis which surrounds the Mediterranean. In eastern Asia oaks are components of the evergreen Himalayan foothill vegetation, spreading from here into mainland and island southeast Asia to the extremes of their range in New Guinea. Through much of this tropical and sub-tropical belt they are confined to montane regions where there are many temperate floristic associations.

4.4.3.1.3. Broadleaved sclerophyll vegetation

Oaks frequently predominate in this vegetation type, found primarily in areas with summer-dry climate: the chaparral of California, and the "maquis" which encircles the Mediterranean (the term "maquis" is used throughout in its most general sense, as short-hand for the shrublands of this zone (di Castri *et al.* 1981), rather than in any more restricted sense). This type of vegetation also extends into areas with some summer rain, such as Arizona, and northern Central America. It also occurs in a restricted part of eastern Asia as woodland/scrub, confined to the dry sunny slopes on the mountains of the East Chinghai-Tibet Plateau.

These vegetation types are very highly generalised, and they all intergrade with each other, though deciduous species are generally restricted to cooler, and evergreen to warmer, areas. In particular, xerophytic deciduous and evergreen tree and shrub oaks may be mixed with each other in transitional zones. A more detailed description of the distribution of oaks within major geographical regions follows.

4.4.3.2. Oak distribution by region

4.4.3.2.1. Western North America

In western North America oaks occur, as trees and shrubs, as components of both deciduous and evergreen woodland or forest, sometimes mixed with conifers; and as components of deciduous and evergreen "chaparral". Although many vegetation maps and descriptions of western vegetation give the impression that woodlands are the only important oak vegetation types Paysen (1980) has emphasised that oaks are sometimes the most important component of vegetation in other areas normally defined as chaparral and coniferous-hardwood. Miller and Lamb (1985) divide the western oaks into three geographical entities, between which there is little overlap of species: the Pacific slope, the Southwest, and the west Texas oaks.

Vegetation types defined as oak woodland are concentrated in the Pacific slope forests in California, especially in the coastal ranges and the western foothills of the Sierra Nevada. At higher elevations, and into the Pacific Northwest, evergreen and deciduous oaks occur as components of mixed forest, with conifers (Barbour 1988; Franklin 1988; Miller and Lamb 1985). Within the Californian foothills oak woodland occurs on the most mesic sites; the dominant vegetation is, however, the broadleaved sclerophyll chaparral, of which oaks are also an important component (Keeley and Keeley 1988). This vegetation type is

characteristic of the mediterranean-type climatic zone in California, and extends south into the mountains of Baja California, where there is some summer rainfall (Axelrod 1973).

The Southwest region of Miller and Lamb also contains oak-dominated vegetation described as "chaparral" in areas with summer rain, but the distinction between woodland and shrubby "chaparral" is somewhat blurred through much of this area. Large areas in Arizona, New Mexico, Utah and Colorado, stretching towards the treeless areas of the east are dominated by deciduous oaks, especially *Q. gambelii*, which spread to the west and southwest of the Great Basin (Keeley and Keeley 1988; West 1988). In this Central and Southern Rockies area oaks also form areas of forest in riparian or canyon communities or as mixed pine/juniper-oak woodland (Peet 1988). In southern Utah evergreen oaks appear in the oak "chaparral"/scrub, and in increasing numbers further south (Peet 1988; West 1988).

In the final geographical division of western North America the oaks of the west Texas region are found principally at high elevations within pine-juniper vegetation (Miller and Lamb 1985).

4.4.3.2.2. Central America

Moving from the "west" into Mexico the diversity of species of oaks increases (Peet 1988), though at first the vegetation types are similar. A further area of "chaparral" with oaks is found on the western slopes of the Sierra Madre Oriental of northeastern Mexico (Keeley and Keeley 1988; Peet 1988), which have a summer rainfall regime. For most of their distribution in northern Mexico oaks are found principally in mixed oak and pine forest.

Oaks extend throughout Central America from Mexico to Panama, to their southernmost extent in the Andes of Colombia. They are principally found in the uplands in this region, in the lower montane (500-2000m) and montane (2000-2500m) belts, which are zones of predominantly temperate vegetation despite their position within the tropics and sub-tropics (Haden-Guest *et al.* 1956; Hartshorn 1988). Oaks are important components of the lower montane canopy (Hartshorn 1988), and may dominate in some regions: in the lower montane region of Costa Rica there are "magnificent stands" of large oaks (*Q. copeyensis* and *Q. tomentocaulis*) (Haden-Guest *et al.* 1956), and in the montane belt here there are remnant trees of *Q. copeyensis* in the moist forests, suggesting that the original forest was dominated by oak (Hartshorn 1988). In the perhumid high-mountain forests there are extensive forests of *Q. costaricensis* (Hartshorn 1988). In contrast to the primarily evergreen oaks of the high-rainfall mountains, the only lowland oak found through Mexico and Central America is in the seasonally-deciduous subhumid forests: the fire-adapted *Q.*

oleoides, which often forms pure stands. It has a disjunct distribution, but may have been more widespread in the past, as this vegetation zone, like much of the rest of this region, has been subject to much human disturbance (Hartshorn 1988).

4.4.3.2.3. Eastern North America

In eastern North America oaks are major components of the deciduous and mixed forests. As in the west, oaks comprise an important part of the arboreal vegetation bordering on the grassland of the plains. In the east they are components of the grassland-forest ecotone, whose boundary is roughly, to the north, in North Dakota and the Great Lakes region, and, moving south, widens through Missouri, southern Kansas, eastern Oklahoma and eastern Texas to the west, and to west Tennessee and Alabama in the east. The vegetation in this zone is a mixture of open canopy woodland or "savanna" above tall-grass prairie with oaks as dominants, in places in association with hickories, or with pines in the south (Greller 1988; Sims 1988). Some oaks occur further west than this zone, as components of the extremities of deciduous forest within the river floodplains and valleys (Greller 1988).

The deciduous forest zone which characterises much of the east stretches from these western borders to reach the east coast in Massachusetts/New Hampshire. To the north, in Maine, and stretching southwest around the eastern Great Lakes, the most northerly of the oaks are found in mixed deciduous/conifer forest. From New Jersey south to North Carolina oaks are present within the Atlantic pine and oak barrens, and to the south and along the Gulf Coasts, sometimes as evergreens, oaks are found within the southeastern pine forest (Christensen 1988; Greller 1988; Sims 1988).

Within the major deciduous forest region their is some zonation of the vegetation, so that oaks are found in association with different groups of genera and species. Moving across the region, the most westerly associations are principally oak-hickory, while to the north and northeast of these, around the south and west of the Great Lakes, oaks are found, often dominating drier sites, in various hardwood associations, principally dominated by beech, basswood or maple. Moving eastwards, the oak-hickory zone grades into a mixed forest, rich in arboreal genera in which oaks are just one of many potential dominants on the more favourable sites. They do, however, dominate the upper slopes, drier sites and areas of rocky outcrops. In the Appalachian mountains a similar mixed vegetation occupies the more favourable sites, though with oaks more usually as dominants; while on the slopes the oaks are now the only dominants, a position they shared with chestnut before it was destroyed by blight in the first half of this century (Greller 1988).

The east and Gulf coastal vegetation is of a very different nature than that of much of the rest of eastern North America (Christensen 1988). On poor soils in the northeast are oak "barrens" or shrubland principally of *Q. ilicifolia*, which are also found on shallow soils in the Appalachians (Christensen 1988; Greller 1988). Other species of oak are found both as shrubs and trees in mixed pine-oak barrens of the northeastern coasts (Christensen 1988; Greller 1988), and in similar communities on sandy soils throughout the coastal region as far as east Texas (Christensen 1988). Oaks are also mixed with pines on more mesic soils throughout the region, usually dominating the understory; and evergreen as well as deciduous oaks are important in the more southerly coastal region. Oaks are important components of mixed evergreen and deciduous forests where these occur on the coastal plain. Low-lying swampy or periodically-flooded areas are a further important component of the coastal plain, and certain tree oaks are frequent components of such communities, usually mixed with other hardwood species, and dominating some areas such as the transition zones to drier areas, as well as some of the swamps.

A final vegetation type in this region in which oaks occur is the maritime forests, found behind the foredunes, where *Q. virginiana* may become established (Christensen 1988). This is one of only two evergreen oaks which occur in the American southeast. Contiguous evergreen forest is not found in this region, but the oaks, along with other broadleaf evergreens occur in small scattered stands from Texas, east and south into Florida, and northwards along the coast to Virginia (Olson 1983).

4.4.3.2.4. Europe and the Mediterranean

In Europe, as in America, oaks are found as components of deciduous and evergreen woodland or forest, as well as components of evergreen broadleaf sclerophyllous vegetation - the "maquis" and its numerous variants, which are equivalent to the chaparral of mediterranean-type California. Much of the following account is summarised from Polunin and Walters (1985).

The deciduous and mixed deciduous-conifer woodland/forest stretches east from the Atlantic coasts of Britain and France into Central Europe, to reach the Black Sea coast and from there stretches northeast to the Ural Mountains. It reaches its northerly extent in southern Scandinavia, and is bordered to the south by evergreen woodland and Mediterranean-type vegetation in the west, and grassland or steppe from the Black Sea eastwards. In contrast to the deciduous woodlands of eastern North America, however, where over 40 species of oak are found (Miller and Lamb 1985) the European oak woodlands are poor in species. Two, *Q. petraea* and *Q. robur*, dominate the northern part of the region, and *Q. robur* is the only species to extend north and east of the Black Sea.

Several other deciduous oaks, however, are important in the more southerly part of Europe, stretching from the Atlantic coast of southwestern France and the northern Iberian Peninsula to the Black Sea borders, north of the evergreen species of the circum-Mediterranean region.

Q. petraea and *Q. robur* may occur in oak woodlands or forest, or in association with other species. In Britain oak woodlands often take the form of oak-hazel coppice or open woodland, while closed-canopy forest is more common elsewhere. Both species may occur as components of beechwoods on suitable soils. Mixed oak and hornbeam woods are especially characteristic of central Europe, but also occur in southwest England and northern France. In the southern Alps oak-chestnut woods are found; and in central and northern Europe*Q. robur* is often found within Scots pine woods.

The deciduous oak vegetation of southern Europe includes local woodlands of *Q. pyrenaica* in the Iberian Peninsula and southwestern France; and *Q. cerris* and *Q. frainetto* which form oak woods in lowland and sub-montane regions of the northern Balkan region, and may also occur as co-dominants in the oriental beechwoods of southeastern Europe. Remnants of woodland, with both the northwesterly oaks and those of southeastern Europe, are also found in the predominantly grassland vegetation of the Hungarian Plain and Danube lowlands.

Between the deciduous vegetation of the Atlantic and central European zones, and the circum-Mediterranean vegetation of evergreen sclerophyll trees and shrubs, occurs a zone of sub-Mediterranean deciduous and semi-evergreen oakwoods, where summer rainfall is low, but not absent as in the true Mediterranean. *Q. pubescens* is the most widespread dominant, replaced by or mixed with other species in the Iberian Peninsula and the Balkans. Both evergreen and deciduous oaks may occur as components of both sub-Mediterranean and Mediterranean pine woods.

Within the true Mediterranean-climate region evergreen and semi-evergreen oak woodland and maquis are some of the most characteristic vegetation types. This type of vegetation is not confined to Europe, and all the circum-Mediterranean vegetation is here considered together. The northern Mediterranean region comprises much of the south and east of the Iberian Peninsula, southwestern France, much of Italy, the southern part of the Balkans, and the Mediterranean islands. Similar vegetation types occur along the Mediterranean coast of Turkey, and south through the Levant to the southeasterly limit of arboreal Mediterranean vegetation in the Gaza area. Westwards, along the North African coast, there are localized areas of evergreen trees and maquis on the north Libyan coast, before this vegetation type becomes continuous from Tunisia to Morocco.

The complex Mediterranean vegetation has been studied in great detail, and though normally described principally as an area of broadleaved sclerophyllous trees or shrubs, deciduous oaks are more common than is implied by this (Le Houérou 1981; Polunin and Walters 1985; Tomaselli 1981a; Zohary 1960). Throughout the circum-Mediterranean region evergreen and deciduous oakwoods, and coniferous woods, are considered to have been the most likely climax community, with much of the shrub vegetation (maquis and its numerous variants) largely the result of the activities of people and their animals (Polunin and Walters 1985). The long human alteration of this area has not, however, only resulted in degradation of woodland to scrub. Many of the areas of oak woodland in this area are managed to produce, for example, cork and timber, as well as acorns for fattening pigs. The dehesa or montado systems of Spain and Portugal are most notable in this respect (see Bainbridge and Felger 1989; Parsons 1962), but Le Houérou (1981) notes that similar combinations of tree products, plus fruits for animals, with an undergrowth of cereal or herbaceous forage, also occur in Morocco (Sous, Rharb), Italy (Sardinia, Sicily), Cyprus, Turkey, Algeria, and Tunisia, and may involve several species of oaks, as well as other arboreal genera. In this way open woodlands have been created and maintained in many areas.

4.4.3.2.5. Southwest Asia

The vegetation of the western part of Southwest Asia bears many similarities to that of adjoining southern Europe and the Mediterranean, often incorporating the same species, though with the addition of many more oak species in Turkey. The deciduous oak-beechwood of southeastern Europe extends along the south coast of the Black Sea through northern Turkey, into the mountains of Armenia and Georgia, with oaks sometimes forming pure stands. The mountains to the south of the Caspian Sea form a similarly mesic area with deciduous oaks, beech and other hardwoods, plus coniferous species (Haden-Guest *et al.* 1956; Zohary 1973). While the mountains to the south of the Caspian, and consequently the vegetation, are very tightly defined and surrounded by steppe-forest, some of which contains xerophilous deciduous oaks, those south of the Black Sea intergrade gradually into the less mesic vegetation of the Anatolian Plateau. Here a steppe-forest vegetation with widely-scattered deciduous trees is found, with oaks an important component. This vegetation is thought to be a remnant of the original park-like woodland, with xerophytic deciduous trees, considered likely to have covered most of Inner Anatolia (Zohary 1973). Towards the east, steppe-like vegetation with occasional remnant trees, including deciduous oaks, stretches to the northern boundaries of the Zagros range, and further east oaks disappear altogether.

At its western end the Anatolian Plateau vegetation intergrades into the more mesic circum-Mediterranean vegetation with forests on the slopes and hills, often of deciduous and evergreen oaks mixed with conifers. This mixed maquis and woodland of the eastern Mediterranean region follows the coast, and spreads inland within the Levant, on to the lower mountain slopes of Syria and the Lebanon, and into the mountains of Israel and Jordan (Haden-Guest *et al.* 1956; Zohary 1973). *Q. coccifera* (often treated as *Q. calliprinos*) is particularly characteristic of this area, often occuring mixed with pistachios, and frequently takes on large tree form, especially in protected places, and in some mountainous areas (Zohary 1960). Above the predominantly evergreen coastal zone, in the mountains, there are also remnants of deciduous forests, with several oaks as important components, mixed with conifers at higher altitudes (Zohary 1973). This vegetation forms the western part of the boundary to the "Fertile Crescent", with the northern and eastern parts made up of a band of oak-dominated forest/scrub which follows the line of the Taurus and Zagros mountains across southern Turkey, northeastern Iraq and western Iran. This band is composed largely of several xerophytic deciduous or semi-evergreen species which spread east and southeast to different extents, with pistachios as common associates. *Q. brantii* forms the most southeasterly extension of oak vegetation in Southwest Asia, extending along the Zagros for almost their whole length. Though much of the Zagros mountains bear "forests" usually of scrub oak vegetation, in remote parts of Kurdistan where they are protected from over-cutting or browsing these species may form closed forest (Haden-Guest *et al.* 1956; Zohary 1973).

4.4.3.2.6. Eastern Asia

From the southern end of the Zagros mountains eastward, no oaks are encountered until the mountainous regions of eastern Afghanistan and the lower Himalayan foothills of Pakistan are reached. Here several species of evergreen oaks occur as dry scrub or as associates of coniferous forest (Browicz 1982, 1986; Gopal and Meher-Homji 1983; Gul and Khan 1982; Haden-Guest *et al.* 1956). The oak vegetation, as a component of mixed evergreen broadleaf-conifer forests, is better developed further east in the Himalayan foothills. In Nepal and Assam the Central Asian and Indian species are joined by others whose distribution spreads into Southeast Asia.

In Southeast Asia itself oaks are largely components of montane evergreen rain forests, where they are often mixed with species of *Castanea*, *Castanopsis*, and *Lithocarpus*, as part of the Fagaceae/Lauraceae forests. As is the case in the Americas, despite their geographical position within the tropics and sub-tropics, the montane forests of Southeast Asia in which oaks are found have temperate floristic affinities, here notably with the warm-temperate flora of China and Japan (Whitmore 1975). The oaks of this region are principally

members of sub-genus *Cyclobalanopsis*, which is restricted to Southeast Asia and the adjoining regions of Malaysia, the Philippines and New Guinea (Camus 1936-1954; Haden-Guest *et al.* 1956; Whitmore 1975).

In southern China oaks are still principally species of the montane zones, as components of broadleaved evergreen forest, mixed with other members of the Fagaceae, such as *Castanopsis* and *Lithocarpus*, or sometimes forming vast areas of pure oak stands as they do in the mountainous southwest (Haden-Guest *et al.* 1956; Hou 1983). Oak species, of sub-genus *Quercus*, dominate the one area of broadleaved evergreen sclerophyllous woods/scrubs of this region, which is restricted to dry sunny slopes on the mountains of the East Chinghai-Tibet Plateau (Hou 1983). The evergreen species of sub-genus *Cyclobalanopsis* become mixed with and eventually replaced by broadleaved deciduous species of sub-genus *Quercus* in the warm- and cool-temperate zones further north, which themselves become mixed deciduous-conifer forests in the northeast. In these areas oaks are no longer restricted to montane zones. In the broadleaved deciduous forest oaks form pure stands, or may be in mixed hardwood stands, with the oaks occupying the more open and light habitats. Many of the deciduous forests of the north are secondary forest, and much of the area is occupied by coppiced woods of *Q. mongolica* (Hou 1983).

Similar south-to-north zonation of oak vegetation, with many similarities at the species level, is found in Korea and Japan, with both having broadleaved evergreen forests in the south, mixed with other Fagaceous genera; with broadleaved deciduous oaks dominating in the north (Haden-Guest *et al.* 1956; Satoo 1983).

The most northerly distribution of oaks in eastern Asia is found in the vast mixed deciduous and coniferous forests of Eastern Siberia, where *Q. mongolica* is the most widely distributed broadleaf tree, though many other genera occur. The vast majority of oak stands are found in the Ussuri River region, and on the coast of the Japan Sea, with the rest along the middle Amur River valley (Haden-Guest *et al.* 1956; Thiel 1957).

4.5. PAST DISTRIBUTION OF OAKS

Oaks have not, of course, always occupied the same areas as they do today, and knowledge of their changing distribution over time is essential when considering potential past human use. Various reconstructions of changes in plant distributions, covering the Tertiary and Quaternary periods, have been attempted, especially within the temperate zone, and some more-or-less global syntheses exist (e.g., Huntley and Webb 1988; Tallis 1991). Here, a brief summary, on a very general regional scale, is made of the changes in the

gross distributional pattern of oaks from the time of the last glacial maximum to the Holocene.

4.5.1. Late Pleistocene and Holocene changes in oak distribution

During the Pleistocene glaciations oaks of the northern temperate regions generally survived in warmer refugia south of their present area of distribution. Within the tropical and sub-tropical regions, where oaks are presently found generally at high altitude, the major changes in their distribution were probably related to the general movement of vegetation belts to lower altitudes during glacial maxima (Tallis 1991), possibly resulting in some constriction of oak distribution between high mountain vegetation and warmer-climate vegetation of the lowlands. The discussion here, however, is confined largely to changes within the present temperate zone.

4.5.1.1. Western North America

Large numbers of species of oaks exist today in California and the American Southwest, and Pleistocene changes in distribution may be partially responsible. The area is physiographically diverse, and would have provided numerous microhabitats for the repeated isolation and expansion of trees as climate varied, with consequent rapid evolution (Thompson 1988). Detailed knowledge of such changes in distribution is uneven, however.

In California there has been little pollen work, and consequently few attempts at vegetation reconstruction (Tallis 1991). However, vegetation zones on the mountains of the coastal ranges and the Sierra Nevada, including forest and woodland communities, are thought to have persisted through glacial periods while displaced to lower altitudes; and mediterranean-type vegetation is thought to have survived in coastal refugia (Roberts 1989; Tallis 1991). *Quercus* pollen is found in the late glacial in both the north and south coast ranges, and mixed conifer-oak forests apparently existed, though at lower elevations than now, in the early Holocene. The current generalised vegetation patterns are thought to have been established in the middle Holocene (Baker 1983).

More detailed vegetation reconstructions have been made for the American Southwest and Mexico. Identifications to the level of species have frequently been possible throughout this area, because of the presence of macrofossil remains preserved in the middens of packrats (*Neotoma* spp.) which persisted through the glacial period, and provide a very local record of vegetation (Betancourt *et al.* 1990; Spaulding *et al.* 1983). Here, as in California, there were apparently altitudinal shifts of vegetation, downwards during the glacial, and upwards

from the early Holocene; as well as a southerly shift, though this is not as marked as in other areas, such as Europe or the eastern United States (Tallis 1991; Thompson 1988). Evergreen oaks were common south of 34° in the late glacial (around 14000 BP). They appear to have formed woodlands in the basin areas now occupied by the Sonoran and Chihuahuan deserts. These oaks did not apparently move north until the very end of the late glacial or the early Holocene (Spaulding *et al.* 1983). Between 11000 and 8000 BP, oaks, together with juniper, dominated mid-altitude sites. By 8000 BP oaks had disappeared from what were now deserts, and modern vegetation patterns are thought to have been established (Baker 1983).

4.5.1.2. Eastern North America

In Eastern North America a considerable amount of palynological work has been undertaken, and mapped reconstructions of the post-glacial changes in vegetation have been made, especially for the Holocene, though the late glacial period is less well known (e.g., Davis 1983a, 1983b; Delcourt and Delcourt 1987; Tallis 1991; Watts 1983; Webb 1988). Oak pollen was present in limited quantities as far north as the southern parts of the boreal forest during the full glacial at around 20000 BP. High oak-pollen values are however, only found south of 34°N at this time, and oak-hickory forest is postulated to have existed in this region (Tallis 1991). Through the late glacial the extreme limit, and the area with higher pollen values, both moved slowly northward west of the Appalachians, though not until the early Holocene east of these mountains, by which time gross vegetational patterns similar to today were in existence (Delcourt and Delcourt 1987; Roberts 1989). Oaks do not, however, reach the levels of dominance shown in modern pollen diagrams until well into the Holocene (Delcourt and Delcourt 1987, 1991). While oaks were spreading northwards, from the early Holocene they were simultaneously pushed eastwards by the developing prairie-forest ecotone (see also Webb *et al.* 1983), and from around 8000 BP oak-pollen values in the coastal plains of the south and east began to diminish. Changes in relative dominance of oaks and other genera continued throughout the range to around 500 BP, and are discussed in more detail in the various publications cited above. Maps reconstructing the spread and changes in dominance of *Quercus* in more detail throughout the east, as well as more general changes in vegetation patterns, are presented by, among others, Davis (1983a), Delcourt and Delcourt (1987), and Webb (1988).

4.5.1.3. Europe and the Mediterranean

The spread of temperate trees into northern Europe from the south was rather slower than in North America, where glacial tundra-steppe and boreal forest remained in position until around 10000 BP. Rapid spread of deciduous trees followed for around 2000 years, by

which time the basic present vegetation pattern was established (Roberts 1989; Tallis 1991). As in North America, however, this does not imply that present plant communities were in existence (Huntley 1988). Pollen maps for individual genera or species groups through the late glacial and Holocene have been produced by Huntley and Birks (1983). These indicate the presence of "deciduous" oaks throughout the Mediterranean at 13000 BP, but concentrated in southern Iberia, the southern tip of Italy, and southern Greece, where oak woodland was probably dominant. "Deciduous" oak pollen is that of members of a group consisting of *Quercus* subgenera *Cerris* and *Quercus* (following classification of Tutin *et al.* 1964), which includes evergreen and semi-evergreen species, notably *Q. suber*. The "deciduous" group showed a slow movement of its extreme limit northward, with gradual increases in pollen concentrations in Iberia, Italy and the Balkans, until 10000 BP, when concentrations in the south increased markedly, and rapid northward expansion began. The expansion is most marked in the western end of the range. At 8000 BP pollen indicates a spread into northern Britain and Europe north and northeast of the Alps, as far as southern Scandinavia, and between 6000 BP and 4000 BP *Quercus* pollen was found further north in Fennoscandia than today (Huntley 1988). High pollen concentrations were still restricted to the south and extreme west, however. Expansion occurred more slowly until 5000 BP, with some contraction of high concentrations in the lowlands between the Alps and the Carpathians, and in Britain and western France. The range remained more or less stable until 2000 BP, when pollen values increased again in Britain and France.

The "evergreen" oak group (members of subgenus *Sclerophyllodrys*, all of which are evergreen) appears in low concentrations at isolated sites in the Mediterranean throughout the late glacial, beginning to show increases in concentration in the east from 9500 BP and spreading into the western Mediterranean and western France by 8000 BP. Huntley and Birks (1983) concluded, on the evidence of the areas in which pollen concentrations first increase, and from the general direction of spread, the likelihood of a major glacial refugium for this group in the eastern Mediterranean. This refugium may have been of considerable size, since it seems to extend within Southwest Asia into the southern Levant (Roberts 1989), where evergreen oaks were a component of open steppe forest during the late glacial. The pattern of distribution of evergreen oaks within Europe appeared to change little for the next 5000 years, except for a gradual increase in pollen concentrations, focussed especially in the lower Rhone Valley, the Dalmatian coast, and southern Greece, with these areas converging by 3000 BP. From 2000 BP there was a withdrawal from the more northerly limits, followed by increasing concentrations in the focus of the range in Corsica and southern France (Huntley and Birks 1983).

4.5.1.4. Southwest Asia

Reconstructions of vegetational changes in the eastern Mediterranean and into Southwest Asia have been summarised by van Zeist and Bottema (1982), though they emphasise that these reconstructions are based to some extent on guesswork, due to the small number of pollen sites, and their scattered distribution over such a large area. Their reconstructions begin immediately after the glacial maximum. From the period between 18000 and 16000 BP continuous forest is postulated only for the south coasts of the Black and Caspian Seas, with steppe forest in the coastal Levant and open steppe with scattered trees in Mediterranean and western Turkey. The next period for which reconstruction is made is from 12000 to 11000 BP, thought to be the warmest phase of the late glacial, with a similar vegetation distribution, though with fewer trees in the north Levant, and greater development of forest in the south, and on the Aegean coast of Greece. At 8000 BP there was continuous forest cover around the Mediterranean, though the southern Levant forest had reverted to open forest. The forest spread some way inland, covering all of Greece, and joined with the Black Sea forest. Forest steppe, or steppe with scattered tree stands, was found stretching as far as western Iran along the Zagros Mountains. By 4000 BP continuous forest cover had spread to cover the Zagros, as well as north to join with the Black Sea forests, so that only the central part of the Anatolian plateau, and the central portion of extreme eastern Turkey remained unforested. Areas of steppe forest occurred on the margins of the forested zone. By this time, van Zeist and Bottema conclude, the forest and forest steppe had reached their present-day extent, though they emphasise that the composition of the forest may have changed subsequently. Oak distribution is not mapped in detail by van Zeist and Bottema, but is a major component of the arboreal vegetation, and often dominates pollen sequences, especially in such areas as southeastern Turkey and the Zagros.

4.5.1.5. Eastern Asia

Detailed reconstructions of vegetational changes through the Quaternary do not exist for much of eastern Asia. Some fairly general summaries are available however, though the emphasis of research has been on vegetational indications of climatic change. Investigations into the Quaternary vegetation of China have been made in increasing numbers in recent years (Hsü 1983; Sun and Wu 1988; Xu 1984). China was not extensively glaciated during the Pleistocene (Hsü 1983), and the main change was a southerly movement of vegetation zones, together with contraction of mesic vegetation in the west as this area became drier. During the glacial maximum, boreal conifer forests dominated in northeast China, and extended further down the mountains in the south than presently. Steppe vegetation spread from northwest into northern China, and has subsequently dominated in that area.

Deciduous forest moved south, with members of the Fagaceae dominating the sub-tropical zone, while the Ulmaceae dominated further to the north. By 9500 BP the deciduous forests had moved back into the northeast, and pollen of *Quercus* dominated from 8000 to 5000 BP, during the warmest part of the Holocene.

The southern edge of the Himalayas is a floristically complex area, and the events which led to the mixing of species (including oaks) with connections in Southeast, Southwest, Central and East Asia are not well understood. Post-glacial changes included a general diminution in the distribution of oak woodland and general replacement by coniferous species, though the extent to which these changes are due to the effects of human activity or to climatic change are uncertain (Vishnu-Mittre 1984).

4.5.1.6. Japan

The late Quaternary vegetation history of Japan has been studied in great detail, and reconstructed by Tsukada (1986, 1988). Pollen of *Quercus* has commonly been identified here to the level of subgenus, with the generally deciduous *Lepidobalanus* separable from evergreen *Cyclobalanopsis*. One exception is pollen of *Q. phillyraeoides*, the only Japanese evergreen member of the former group. Japan was not covered with ice even at the glacial maximum, around 20000 BP, though ice caps were present on high mountains in Hokkaido (the northern island) and central Honshu. Coniferous forests covered most of the land, with mixed conifer and deciduous broadleaved forest, of which *Quercus* subgenus *Lepidobalanus* is thought to have been a component, around the coasts as far north as northeastern Honshu. Warm-temperate evergreen broadleaved forest was present in the extreme southerly coastal region. Pollen of subgenus *Lepidobalanus* begins to increase in numbers in the late glacial, around 15000 BP, while around 13000-12500 BP its distribution expanded rapidly inland from the coast, and then northward around 12000 BP. Tsukada estimates that *Lepidobalanus* trees reached their northernmost extent, in Hokkaido, by around 8000 BP. The evergreen trees of *Quercus* subgenus *Cyclobalanopsis* began to spread through Kyushu (the southernmost island) during the late glacial, and into southern Honshu between 10000 and 7000 BP, moving north at first along the coasts. Other components of the evergreen forests, such as *Castanopsis*, spread north towards the end of this period. By the mid-Holocene (between 7000 and 4000 BP) broadleaved evergreen forests dominated in the southwest, and broadleaved deciduous forests in the northeast, though considerable changes in the distribution and dominance of individual species subsequently occurred, in response to both climatic changes and human activities.

4.6. THE EFFECTS OF ENVIRONMENTAL DISTURBANCES ON OAKS

In many discussions by archaeologists and others interested in environmental change, the deleterious effects on oak and other trees of environmental disturbances such as fire, cutting of trees, or animal browsing have been emphasised. However, not only has the role of "disturbance" within "natural" ecosystems become more accepted recently (see, e.g., Blumler 1991), but oaks are in fact more resistant to such effects than are many other species, and show certain adaptations to disturbance. Many oaks are capable of sprouting vigorously from root-crowns, stumps or within the canopy when cut, burnt or browsed. This response is particularly vigorous in oaks with shrubby habit found in regions subject to frequent disturbance, but is not confined to these areas. Oaks are also generally shade intolerant (Miller and Lamb 1985; Penistan 1974), and reproduction, both vegetative and by seed, can be enhanced by opening up vegetation cover. Shade intolerance is not generally a common feature in species which occupy the dominant, or climax, position in undisturbed ecosystems, and it has been suggested that where oak species and woodlands appear as dominant worldwide this is due largely to disturbance by fire (Spurr 1964, cited in Komarek 1974).

4.6.1. Effects of fire

The extent to which oaks are affected by fire varies between species and ecosystems. Chaparral or maquis landscapes, as well as their extensions into surrounding shrublands, in western North America and the Mediterranean and Southwest Asia, are widely acknowledged as having a certain dependence on burning (natural or human-induced) or browsing (by wild or domestic animals). The role of both natural and human-induced burning in both producing and maintaining other ecosystems has been more recently acknowledged among those involved in woodland or forest management (see papers in Kozlowski and Ahlgren 1974).

4.6.1.1. Western North America

The broad-sclerophyll vegetation, or chaparral, of California and adjacent areas is generally considered to be a fire-adapted type, and to be maintained principally by fire (Keeley and Keeley 1988). Several evergreen and deciduous shrub oaks of the California chaparral regenerate rapidly after fires by sprouting, as do many other species of this vegetation type (Biswell 1974; Griffin 1980b). Unlike many other chaparral species, however, oaks are not fully pyrophytic, because fire is not required to induce germination of seed; and acorns, in fact, are very easily destroyed by heat. Despite the fact that their reproduction in fire-influenced habitats is therefore largely vegetative, oaks are nevertheless frequently a

dominant component. As is typical of many chaparral plants, a large proportion of the biomass of shrub oaks is concentrated in the root crown, enabling it to resprout vigorously and relatively frequently, the root-crown enlarging with each fire so that the number of resprouted stems increases (Rundel 1980). Oaks may also have some advantages over most other chaparral plants. Green (1980) found that California shrub oaks survived fires better than other components of broad-sclerophyll vegetation because they contained less volatile substances, had a higher moisture content, and contained a lower ratio of highly-flammable dead wood. Biswell (1974) notes that individual members of a semi-deciduous shrub oak species, *Q. dumosa*, may live for centuries, constantly regenerating, if fires are not too frequent.

The response of Californian tree oaks to fire is more varied. Much of the older literature, and more recent literature where oak is being considered largely for its value as timber, implies that oak trees and woodlands are threatened by burning. However, in determining the extent to which fire is harmful or otherwise, several points must be considered. Naveh (1974, 414) separates responses to fire of woody plants into "positive feedback" and "negative feedback" mechanisms. Positive responses may be vegetative, or relate to seed dissemination or germination; while negative responses consist primarily of the development of protective measures, notably thick bark.

Most Californian species are rather thin-barked, with a few exceptions, such as the evergreen *Q. agrifolia* and *Q. engelmannii*, which are considered to be fire-resistant (Green 1980; Plumb 1980). In many tree oaks however, fire can fairly easily damage trunks, stems and canopy, killing some or all of the above-ground parts of the tree, as well as producing fire scars which permit disease to enter (Green 1980).

The most significant behaviour of California oaks is thus a "positive feedback mechanism" - sprouting. Because trees do not contain such a large proportion of biomass below ground, they are less likely to be capable of maintaining the frequent and vigorous stump-sprouting characteristic of shrubs. Nevertheless, sprouting from the root crown does occur when the tree is top-killed, and regeneration in this way has apparently been responsible for the creation of many even-aged clumps of oaks (Kerns 1980; McDonald 1980; Tappeiner and McDonald 1980). When the tree is less severely damaged sprouting may also occur from epicormic buds higher on the stump or within the canopy, depending on the extent of damage, and the species (Griffin 1980b; Minnich 1980; Plumb 1980; Rundel 1980).

Evergreen oaks are generally considered to be more vigorous sprouters than deciduous species (Passof *et al.* 1985). The closely-related evergreen tan oak (*Lithocarpus densiflora*), is noted for rapidly dominating sites after fire or logging activities, as it both

sprouts vigorously, and produces prolific seed with fast-growing seedlings (Jepson 1923; King and Radosevich 1980). Jepson (1923) however, noted that it was members of sub-genus *Erythrobalanus* which were the most vigorous sprouters, while those of *Lepidobalanus* sprouted less vigorously, declining or ceasing especially with increasing age. Evergreen and deciduous habit, as well as shrub and tree form, in the Californian species, cross the taxonomic boundaries, and it is difficult to determine to what extent fire is harmful or beneficial in any one species (Rundel 1980).

Plumb (1980) examined fire resistance for four species of tree oak, and considered damage to two evergreen species, *Q. chrysolepis* and *Q. wislizenii*, to be so severe that the use of fire could not be recommended in their management, while damage to *Q. kelloggii*, a deciduous species, (and a member of sub-genus *Erythrobalanus*), was not so severe. Passof *et al.* (1985) noted that *Q. kelloggii* appeared to have a positive sprouting response to fire similar to that of many of the evergreen oaks. Tappeiner and McDonald (1980), however, found that trees of this species were severely damaged by crown fires, and even ground fires unless mature.

Great intraspecific variability is characteristic of oaks (see 4.3.4.), and may also be seen in fire response. It seems likely that fire ecotypes of some species may exist, in response to the strong selective pressures exerted by burning. *Q. chrysolepis*, *Q. agrifolia*, *Q. garryana*, *Q. wislizenii*, and *Lithocarpus densiflora* all exist in tree form in woodland, and in shrub form in chaparral, the forms having been considered as separate sub-species by some (e.g., Jepson 1923).

Apart from the fact that study of the response to fire is complicated by such inter- and intra-specific differences, as well as factors such as the balance between "positive" and "negative" responses, part of the reason for apparent differences may be related to the different interests of those carrying out the study. Those interested in oaks for timber, for instance, do not favour trees which have been damaged and resprouted epicormically. Such sprouts, especially when high on the stump, tend to be easily broken by wind or snow, and are prone to rot from the stump (Tappeiner and McDonald 1980). Resprouting may therefore be characterised by some as a poor response to fire.

Differences in tree size and age may affect both fire resistance and response. In general larger trees tend to be more resistant to fire damage than smaller ones, both as a result of thickening of bark and increased canopy height (Plumb 1980), while smaller and younger individuals are generally able to sprout more vigorously than older specimens (Passof *et al.* 1985). In some species, such as the deciduous *Q. douglasii* and *Q. lobata* (both sub-genus *Lepidobalanus*) sprouting is particularly poor in older specimens (Griffin 1980b; Jepson

1923; Passof *et al.* 1985; Rundel 1980). In the case of young trees, fire may actually encourage growth. Tappeiner and McDonald (1980) suggested that fire amongst oak seedlings may destroy the low scrubby growth which can be maintained by browsing for several decades, and perhaps permit growth of one vigorous sprout which can quickly grow beyond browse height.

Minnich's (1980) study of *Q. chrysolepis*, one of the most morphologically-variable of California oaks, is interesting in illustrating the potential differences in fire ecology which can exist within the oaks. In chaparral, found on exposed slopes, it takes on a shrub form, due to its vigorous sprouting ability. In less fire-exposed areas, such as sheltered canyons, it forms woodland. Minnich noted that despite the fact that *Q. chrysolepis* is thin-barked and slow-growing as a tree, and in some circumstances is easily top-killed, the woodlands it formed seemed to have a considerable resistance to fire. He suggested that this was due to the low quantity of dead leaves present in the crown, the large ratio of living to dead biomass, and the height of the canopy above ground fires (also noted by Plumb 1980).

There is, in fact, much evidence that fire itself may be an important part of oak woodland ecology. The adaptations of the Sierran forests to frequent, largely lightning-induced fires, are well known, and the area is characterised by wide spacing of individual trees, with spacing apparently closely related to age of stands (Jepson 1923; Weaver 1974). Although the majority of species involved are various conifers, *Q. kelloggii* is an important component, as well as occurring as large individual trees in adjacent, frequently-burned, chaparral. Much evidence for the survival and maintenance of oaks in the form of open woodland within fire regimes comes from reports of early travellers and settlers in California and elsewhere in the West, (see Biswell 1974; Jepson 1923; Rossi 1980; Weaver 1974) who described regular burning practices of the Indians. This burning, whether "natural" or human appears to contribute to the open, park-like appearance of many areas, by the clearance of scrub and dead vegetation, preventing both the development of denser wooded vegetation, and accumulations of large quantities of flammable material which could result in fires intense enough to destroy trees and lead to chaparral formation. Together with the reduction in competition, such factors may actually favour the growth of large individual trees (Jepson 1923). Fire-control policies subsequently adopted have enabled scrub and dead vegetation to build up, resulting in more intense burning when fire suppression fails, which is more likely to seriously damage trees.

The reasons why Californian oaks form woodlands in some areas and chaparral in adjacent areas are evidently dependent on a large number of factors. While inter- and intra-species variation in response to fire is important, existing tree or stand form, and vegetation type,

may themselves be significant. The relation of oak vegetation to fire can obviously therefore be a very complex and dynamic one; and fire can either maintain a stand, or lead to an alteration in its composition or structure, depending on its frequency and intensity, the latter being partially dependent on the former, as well as on the existing vegetation type. The almost symbiotic relationship between chaparral and fire described by Biswell (1974) may thus have more subtle manifestations in other vegetation types.

4.6.1.2. Eastern North America

The fire-relations of much of the Eastern Woodlands have been less well studied than those of the west, and most of the work on fire ecology has been undertaken in peripheral parts, with little in the greater central part of the area (Komarek 1974). As in the west, there is a tendency for older literature, especially that of foresters, to consider fire as a problem, while more recent works consider fire as another ecological factor to which some species at least may be well-adapted.

Komarek (1974) noted that in the deciduous forest of the southeastern United States, on the Appalachians and to the west, fire, caused largely by lightning, may burn over relatively small areas, creating a mosaic effect. Experimental frequent burning has been carried out in recent times, and creates a park-like landscape with scattered trees. The reappearance of many grassland species within these areas led Komarek to suggest that such frequent burning may have been common throughout the deciduous woodlands in the past, and that open areas may have also been more widespread than is currently the case. Fire suppression policies over much of the Eastern deciduous woodlands have altered the balance of vegetation so that it is more difficult to reconstruct the likely past fire ecology of these regions.

Komarek does not comment on the relative success of oaks within this area. Fender (1976, cited in Green 1980) considered Eastern woodland oaks to be so sensitive to burning that fire could not be recommended in their management. However, in the Northeast, Little (1974) noted that in comparison with other hardwood species oaks are thicker-barked, and sprout more readily; and Wood (1938) notes that the oak forests of this area are largely of coppice origin, relating to past cutting as well as fire. As in the West, there is evidence for a previously more open park-like vegetation maintained by Indian-burning (Day 1953; Little 1974; Russell 1983), and oak stands which in the past had been favoured by fire regimes are now being taken over by more shade-tolerant species (Little 1974). On the western edge of the deciduous woodlands, where fire is thought to have helped in the formation and maintenance of the Prairies, the thick-barked and deep-rooted *Q. macrocarpa* is fire-adapted

and survived further into the prairies than other trees while Indian burning was common (Miller and Lamb 1985).

Fire is a more common and well-studied phenomenon in the coastal plains from the Northeast to Texas. Climatic factors mean that fires here are frequent and intense. The fire ecology of the pine-oak woodlands is perhaps the best known, though other coastal woodlands of this area, both deciduous and evergreen, of which oaks are often important components, are also subject to frequent fire (Ahlgren 1974; Christensen 1988; Greller 1988; Komarek 1974). The balance of pine and oak changes with fire frequency and intensity, and pines dominate in the more severely burnt areas (Komarek 1974; Little 1974), but oaks are undoubtedly fire-adapted. The coastal pine-oak woodlands are subject to the most intense and frequent fire, and tree oaks which do not produce acorns until the sprouts are around twenty years old are present only in small quantities. The shrub oaks found here, however, some of which are apparently fire-adapted ecotypes of species elsewhere found as trees (Christensen 1988), are well adapted to such conditions. They not only regenerate vigorously by sprouting, but acorns can be produced at a very early age, as soon as three or four years after a burn (Little 1974, see also 4.6.4.).

4.6.1.3. Mediterranean

The Mediterranean maquis, like the chaparral of western North America is a fire-adapted vegetation type, as has been emphasised by Naveh (1974), Godron *et al.* (1981), Le Houérou (1981), and Trabaud (1981). As in California it is the evergreen species which appear to grow in closest relation to fire. Le Houérou (1981) notes that in this region deciduous forests are less likely to be burnt than are evergreen forest and maquis, because they tend to occupy areas with higher rainfall. He suggests, too, that those forests in areas susceptible to fire have already been transformed into evergreen forest or maquis.

The emphasis on such destruction of woodland by fire, and on maquis vegetation as a "degraded" type has been even greater in the Mediterranean than California (see, for example, Lossaint 1973; Tomaselli 1981b). However, some have commented on the potentially beneficial effects that fire can have on Mediterranean vegetation, as well as on the possibly distorted perception of fire, related to its frequent association with other disturbance factors such as grazing, browsing, extraction of firewood/charcoal, and clearance (Le Houérou 1981; Naveh 1974; Trabaud 1981). The long history of intensive habitation and associated human activities in the Mediterranean, and especially the browsing activities of domestic animals, makes it more difficult to determine the effects of fire, and its natural regularity and intensity is little understood (Le Houérou 1981).

Responses of oaks are similar to those described for California. *Q. coccifera* (sometimes given as *Q. calliprinos* in the eastern Mediterranean), is categorised as an obligate, and very vigorous, root-crown sprouter (Naveh 1974), which often dominates land after fires. According to Le Houérou (1973; cited in Naveh 1974) *Q. coccifera* maquis has been in equilibrium with periodic burning for centuries. With too frequent burning, however, even this species cannot survive, though heavy browsing on the lush sprouts may contribute to this destruction. This species occurs as a well-developed tree where disturbance is not too severe (Naveh and Dan 1973; Zohary 1960). Though it is the species most frequently characterised as fire-adapted, Trabaud (1981) has emphasised the fact that response to, and recovery from, fire in other species can be good, especially when other disturbance factors are not involved. The evergreen *Q. ilex*, although very thin-barked can survive as woodland when fires are not too intense, and will sprout epicormically from the stump, or from root crowns if damage is more severe, taking on shrub form (Trabaud 1981). *Q. suber* woodland can also be maintained when fires are not too intense or frequent (Trabaud 1981). This species possesses very thick bark which makes it resistant to fire damage, and it takes over, in tree form, from *Q. faginea*, in the western Mediterranean where burning has occurred (Le Houérou 1981).

To what extent fire-adapted oak woodland/parkland similar to the Californian types may have been maintained in the past is uncertain, and has been very little studied. Although analogies are frequently drawn between the two regions, Naveh (1974) points out one important modern-day difference. Natural fires, set by lightning, are very much less common in the Mediterranean than in California (see also Trabaud 1981), though to what extent this is due to differences in other ecological factors (such as heavy grazing, or increased percentage of human-set fires) is again uncertain. Another difference is the absence of true oak shrubs - all those species (with the possible exception of *Q. fruticosa*, confined to the Iberian Peninsula) which take on shrub form are capable of also growing as trees (Rackham 1982; Tutin *et al.* 1964).

4.6.1.4. Europe

The past and potential role of fire in European woodlands is even more uncertain than in the deciduous woodlands of eastern North America, as they have suffered more from recent human alteration and destruction. In Europe, the role of fire is frequently discussed by those interested in past environment in relation to land clearance and shifting cultivation. The long history of management of trees for various products by coppicing, pollarding, and similar practices means that the potential role of burning in this respect has been little considered. Rackham (e.g., 1988) considers that European woodlands, in contrast with North American ones, possess only one species, *Pinus sylvestris*, that will burn readily,

and has inferred that burning would not be a suitable method of land clearance. Despite Rackham's comments, the analogies in terms of generic composition between Europe and the Eastern Woodlands (as well, possibly, as the temperate deciduous woodlands of Eastern Asia) suggests that fire ecology in the two regions might have similarities. European oaks are certainly capable of recovering from burning - Jones (1959) noted that seedlings and saplings whose tops are fire-killed can produce vigorous sprouts from ground level. Older trees are protected by thick bark from burning, while younger ones may be damaged and permit decay, a situation analogous to the responses of American oaks.

4.6.2. Effects of mechanical damage on oaks

This section includes consideration of the effects of both cutting of trees and of browsing by animals. It seems likely that this type of damage would elicit responses in oaks similar to responses to fire damage, when analogous parts of the plant are affected (such as clear-cutting being equivalent to top-kill), though this is not entirely certain. Certainly much of the literature referring to sprouting does not distinguish between responses to cutting or to fire.

Van Dersal (1938) listed the qualities of North American oaks, and many of the species are recorded as coppicing, or sprouting freely. Examples include many species of the Eastern Woodlands, of both the *Lepidobalanus* and *Erythrobalanus* groups; as well as many of the Californian species whose sprouting qualities have been discussed in 4.6.1.1. Fowells (1965) and Miller and Lamb (1985) also include sprouting capacities in their descriptions of North American trees.

There are differences between species in sprouting capacity, including notably some members of *Erythrobalanus* recorded with poor sprouting ability, though this may be in contrast to others of the sub-genus. The evidence generally provides some support for Jepson's (1923) observations, based on Californian oaks, for the greater sprouting vigour of members of sub-genus *Erythrobalanus* (see 4.6.1.1.). Members of *Lepidobalanus* are generally recorded by Van Dersal as stump-sprouters (though Miller and Lamb's descriptions suggest they may also coppice), which is again analogous to observations of the Californian members of this sub-genus. Jepson (1923) noted that *Q. douglasii* and *Q. lobata* both sprouted poorly from the root crown, but sprouting was greatly enhanced if trees were cut high, above the first branches. Interestingly, the only evergreen species included, *Q. virginiana*, is a member of sub-genus *Lepidobalanus*, and like the other members, is recorded as a stump-sprouter. This species does, however occur in shrub form, and Miller and Lamb (1985) note that it regenerates vigorously from the root-crown

as well. Sprouting ability generally is emphasised as being either exclusively from, or more vigorously from, younger trees.

The ability to sprout or coppice freely has also been noted in European deciduous forest species, such as *Q. petraea* and *Q. robur*. Sprouting can be vigorous, especially in the former species, in individuals up to around 30 years though sprouts may be produced more weakly to a much greater age (Jones 1959). Jones also comments that stems arising from below ground level are more vigorous than those which sprout higher up. The strong sprouting ability of evergreen oaks in the Mediterranean, whether after fire or cutting, has been noted (Debazac 1983, see also 4.6.1.3.), though Quézel (1981) has emphasised the important, and often unacknowledged role that deciduous oaks may play in the maquis landscape. Personal observation in southeastern Turkey has shown the ready sprouting ability of deciduous species such as *Q. brantii* and *Q. infectoria* ssp. *boissieri*, both in coppice form and from upper branches in response to cutting higher on the tree.

Further inferences about the responses of oaks can be derived from similar practices known or recorded in many parts of the world. The fact that oaks have frequently been managed as a renewable resource, for such products as wood, bark, and leaf fodder, implies their ability to respond positively to damage, whether deliberate or accidental.

4.6.3. Combined effects of fire and mechanical damage

It is difficult, in many cases to examine the effects of cutting, browsing and fire separately, as they often occur more or less simultaneously, and may be synergistic. Though such synergism is generally seen as having a negative effect on oak regeneration (especially in maquis or chaparral vegetation, as indicated in 4.6.1.3.), this does not have to be the case. Thus two factors in combination may potentially have a positive effect on oak growth.

Both fire and cutting can be responsible for the production of sprouts which may be within reach of browsing animals. Such sprouts are lush and are more attractive to animals than the relatively spindly growth of slow-growing seedlings (Jones 1959; Moore and Johnson 1967). Both these authors provide evidence suggesting that quite subtle differences in the extent of browsing may control the balance of growth. Sprouts can grow rapidly and become quickly less palatable, leaving any seedlings in an area to continue to be browsed. Moore and Johnson also note that shoot sprouts are more succulent than root sprouts. In an area with variable fire damage, animal browsing might concentrate on the former, assisting the root sprouts' ability to grow out of reach. With heavier browsing pressure shoots may be kept within reach longer, with seedlings consequently ignored and permitted to grow.

With even heavier pressure, presumably both sprouts and seedlings would be kept in check.

As noted previously (see 4.6.1.1) sprouts produced after burning may be vulnerable to disease, and Murray (1974) has noted that coppiced oaks in Britain, especially in their first few years, are vulnerable to attack by oak mildew. In North America burning stumps after cutting has been found to make them less susceptible to rot, by encouraging sprouting from as low as possible (Little 1974).

4.6.4. Effects of environmental disturbance on acorn production

Although a considerable amount of information exists on the effects of cutting, burning, and browsing on the survival and regeneration of oaks, little of this is concerned with the effects of such factors on acorn production.

Much of the information that does exist relates to shrub oaks, which often characterise environments affected by fire, heavy browsing, or frequent cutting. Species in such environments can survive either solely by vegetative reproduction, principally sprouting, or by producing seed within the average period between disturbance episodes. Both these mechanisms are found in oaks (see 4.3.4.5. and 4.6.1.1.). The indistinct boundary between shrub habit and tree habit in many species of oaks has been discussed in 4.6.1., and oaks may have different forms in different environments. However, it is those species which are only found as shrubs which are generally recorded as being capable of rapid production of acorns on young shoots, either as seedlings or as sprouts grown in response to disturbance.

Examples include *Q. pumila*, a shrub oak of the frequently-burnt pine barrens of the American Southeast, which sprouts vigorously after burning (Johnson and Landers 1978; Miller and Lamb 1985). Johnson and Landers found that acorn production was at its highest two years after burning in a pine plantation, but declined markedly after that, though in younger pine plantations production of acorns increased up to at least ten years. Two other shrub oaks present, *Q. virginiana* var. *geminata* and *Q. virginiana* var. *minima*, also bore acorns in this environment, while seven species of tree oak did not.

Q. ilicifolia, which occupies a similar ecological position to that of *Q. pumila* in the "oak barrens" of the Northeast, and which generally produces good crops by at least the age of nine (Wolgast 1978), produces shrubby growth in response to fire, and can produce acorns within three years of cutting or fire, also in increased numbers (Miller and Lamb 1985; Wolgast and Stout 1977a). Little (1974) also comments on the adaptation of this species,

together with *Q. prinoides* and *Q. marilandica*, to the frequent, intense fires of this region. Interestingly *Q. marilandica* is one of the species recorded by Johnson and Landers (1978) in the Southeast as a tree oak not capable of producing acorns in a frequently burnt environment. This is a widely distributed species, recorded by Miller and Lamb (1985) as a poor sprouter, which can, however, take on either tree or shrub form depending on the environment.

In California Biswell (1974) notes that most woody plants of the chaparral (of which shrub oaks are an important member) will produce seed within three to five years of a fire, which is the usual minimum interval between burning.

The oak species of the Mediterranean which dominate in areas subject to frequent burning or cutting, or heavy browsing, appear to do so largely because of their positive vegetative response. *Q. coccifera* (including *Q. calliprinos*), with the most most marked positive response, is categorised with the "obligate resprouters" of this environment rather than the "facultative resprouters", which are able to produce seed on young-growth sprouts (Naveh 1974). This species is another which can take on both shrub and tree form. However, Rackham (1982) records that *Q. coccifera* will produce a full crop of acorns at any size greater than 60 cm high. It may be the absence of opportunities for seedling growth rather than the absence of acorns which explains Naveh's categorisation.

There is little quantitative information on the fruiting response to cutting or burning of oaks which more fully adopt the tree habit. Little (1974) notes that species such as *Q. alba*, *Q. coccinea*, *Q. prinus*, and *Q. velutina* of the American Northeast will produce acorns on sprouts which are 20 years old. This is the same as the minimum seed-bearing age for these species (USDA 1974), but it is not clear whether these figures also relate to sprouts. In Europe Maximov (1930, cited in Wood 1938) noted earlier production of acorns on vegetatively propagated trees than on those derived from seedlings; and others have noted earlier production on either coppice shoots or rapidly-growing trees (Evans 1988; Shaw 1974). Acorns may be produced on coppice shoots of *Q. petraea* or *Q. robur* at the age of 10-15 years, as a consequence of shortening of the juvenile period (Jones 1959; Longman and Coutts 1974). None of these sources comment on whether production by coppice shoots is more regular or abundant than that of seedling trees.

Sprout growth produced in response to opening up of vegetation cover can be relatively dense, with narrow crowns not conducive to heavy acorn production (see Miller and Lamb 1985). Tappeiner and McDonald (1980), in a study of the development of even-aged stands, resulting from felling, of *Q. kelloggii* suggested that thinning of sprouts after several years enabled the development of fully-crowned trees, which would be likely to

produce abundant acorns at a much earlier age than the narrow dense sprout crowns which otherwise tended to develop. Kerns (1980) made similar comments regarding the same species, and noting that regularly-productive broad crowns did not develop naturally until an age of 80 or more years. Thinning is generally recommended by foresters to increase flowering and seed production (Evans 1988). Some studies provide indications about acorn production in environments with varying amounts of openness. Flegg and Bennett (1974), in southeast England, noted a larger number of birds using areas with mature closed-canopy standard oaks, as opposed to oak coppice, partially as a consequence of the far greater production of acorns. Bird use of open "glades" with standard oaks scattered through a mixed scrub and grassland was even higher, although the area of oak canopy was obviously smaller. They do not comment on the relative acorn production in open as opposed to closed-canopy areas. However, many factors other than acorn production are obviously involved here. Kerns' (1980) found that mature stands of *Q. kelloggii* were superior wildlife habitats to either dense younger stands, or to any of the edge habitats which they created with surrounding vegetation, again principally because of the greater number of acorns produced.

One potential response of oaks to disturbance is suggested by Jepson's (1923, 105) description of "jayhawking" of the tan oak *Lithocarpus densiflora*. This term was applied to removal of bark, for tanning, from young trees or sprouts. The trees would take two seasons to die, in the last of which they would generally produce an exceptional crop of acorns. This might seem a potentially destructive means of producing a reliable crop, but in this species at least, vigorous resprouting from the root crown subsequently occurs, and within 15 years or so another crop of sprouts is ready for stripping, with individual clumps persisting indefinitely, though whether these continue to produce acorns is not recorded.

Though selective cutting of trees has long been acknowledged as a means to open up oak woodland canopy, use of fire, as noted in 4.6.1., has in the past been considered unacceptable, because of potential damage to living trees. However, increasing understanding of the likely past fire ecology of many areas, and the capacity of oaks to withstand or respond positively to fire has meant that even in the Eastern Woodlands of North America controlled burning has been recommended as a means of opening up and improving wildlife habitats, with one consequence being improved acorn yield (Miller and Lamb 1985).

CHAPTER 5. THE ACORN - AN INTRODUCTION

5.1. INTRODUCTION

Models of acorn use have frequently drawn upon various biological characteristics of the acorn (see Chapter 2), and some understanding of the underlying reasons for these can aid in the understanding of the acorn as a food resource, as is discussed in Chapter 8. This chapter constitutes an introduction to the physical and physiological characteristics of acorns. The following chapter covers those biochemical and nutritional characteristics which relate to the potential role of acorns as a food source.

5.2. THE ACORN - MORPHOLOGY AND ANATOMY

5.2.1 Introduction

Within the Fagaceae the genus *Quercus*, together with *Lithocarpus*, and some members of *Castanopsis*, are characterised by the possession of one flower, and subsequently one fruit, per cupule. The "acorn" is not therefore confined to *Quercus*, but the following discussion, unless indicated otherwise, is. Acorn anatomy and morphology has been described and illustrated by numerous authors, and summarised by Gassner (1973), Korstian (1927), Ward (1892), Winston (1956), Winton and Winton (1932), and, for the developing acorn, Kaul (1985), and Langdon (1939). The following account is summarised from these. While it is often necessary to have acorns to identify oaks to species level, it is also helpful in some cases to examine vegetative structures of the trees in order to allocate acorns to species. The following discussion, however, attempts to provide some idea of those features which have been, or might potentially be, of use in the identification of acorns from archaeological contexts.

The acorn is a type of nut - defined as a hard, dry, indehiscent fruit, derived from a unilocular ovary of fused carpels, in which all the ovaries except one abort, so that the fruit is one-seeded. According to Kaul (1985) the acorn is more precisely a calybium, as it derives from an inferior ovary (cf. also Langdon 1939), and the pericarp is fused with the surrounding floral parts, but, as Esau (1953) points out, there is little agreement on the definition and classification of fruits, and the definition of pericarp is narrowed or expanded depending on authority. Though the acorn shell is, strictly speaking, fused pericarp and hypanthium, in the anatomical descriptions mentioned above it is invariably referred to as pericarp, and that convention is followed here.

5.2.2. External morphology

The acorn comprises the seed, of embryonic axis and cotyledons, and the shell, or pericarp. It is surrounded by, or in some cases enclosed by, the cupule.

The cupule consists of successive layers of sclerified and suberized bracts, the cells of which develop increasing quantities of crystals and tannins as they age. The bracts surround a central axis, to which the pericarp is joined at its abscission scar (the basal disc of the acorn shell), and through which the vascular tissues pass. The cupule of *Quercus* may be covered with scales of varying sizes (sub-genus *Quercus*), or may have concentric or spiral lamellae (sub-genus *Cyclobalanopsis*). Characteristics of these features, including the extent to which scales are adpressed or spreading, together with the extent to which the cupule covers the acorn, and the hairiness of the cupule (inside and out) can be taxonomically diagnostic (see also Barnett 1944).

Acorn size, the relation between acorn and cupule size, and the degree of enclosure of the acorn, may also vary considerably between species. Kaul (1985) examined these features in some Southeast Asian oaks, and though they appeared to show few ecological correlates, it is possible that they could be taxonomically diagnostic, at least in combination with other features. The external morphology of the pericarp varies, especially in the shape of the apical end, which sometimes bears the remains of the stigma. The size, and perhaps the shape, of the basal attachment scar of the shell may also be taxonomically distinctive (Barnett 1944).

5.2.3. Internal morphology

The kernel itself consists usually of one non-endospermous seed, though up to six may be found in one acorn, since the ovary is three-celled, with two ovules in each cell. As noted above, usually only one ovule develops, and the position of the aborted ovules is taxonomically diagnostic. In *Cyclobalanopsis* and *Erythrobalanus* (as well as in the closely related genus *Lithocarpus*) they are found at the apex of the acorn, while in other groups they occur laterally or at the base (Camus 1936-1954; Kaul 1985; Rehder 1947; Trelease 1924, cited in Korstian 1927).

At the apical end of the acorn the two plano-convex cotyledons are joined via their rudimentary petioles to the hypocotyl. Attached to this is the radicle, which lies towards the apex, and the plumule, which sits between the petioles and points towards the base of the acorn. All these tissues are clearly differentiated at the time of maturation of the acorn, and

according to Sargent (1895, cited in Korstian 1927), the radicle of the red oaks is longer than the cotyledon petioles, while in most of the white oaks it is shorter.

The outer surface of the red oak cotyledons may be heavily grooved, and the testa in all cases adheres closely to the surface, and is thickened over any grooves.

One feature found in some acorns is the presence of septa, formed from sclerified placental partitions. They appear particularly in *Cyclobalanopsis*, and occasionally in *Erythrobalanus* (Kaul 1985).

5.2.4. Anatomy

The pericarp consists of five layers: a heavily cutinized epidermis of cuboidal cells; a single, and sometimes discontinuous, layer of thin-walled parenchyma cells, containing hyaline crystals, probably of calcium oxalate; a layer of thick-walled sclerotic cells, varying inwards from elongate (four times as long as broad) to iso-diametric; a parenchyma layer of varying thickness (in some members of *Lepidobalanus* forming the major part of the shell), with slightly thickened pitted walls and minute air spaces, interspersed with groups of stone cells; and an inner epidermis of elongated cells, barely distinct from the parenchyma, but in *Erythrobalanus*, and some members of *Protobalanus*, bearing hairs which form a felty layer on the inside of the shell. Korstian (1927) examined the relative thicknesses of some of these layers in acorns of two white oak and three red oak species, and found the cutinized epidermis to be slightly thicker in *Erythrobalanus* than *Lepidobalanus*, with the underlying sclerotic layer showing a similar, but more pronounced difference. Added together these are thicker in red than in white oaks, though the maximum and minimum ranges of species in the two groups overlap. The underlying parenchyma layer varied in thickness among acorns of the two groups, though it tended to be thicker in the white oaks (extremely so in *Q. prinus*), so that total shell thicknesses were not distinctively different between the two groups.

The testa of the acorn is usually a thin layer consisting of a few rows of thin-walled cuboidal parenchyma cells. A single layer of epidermal cells surrounds the mass of large thin-walled iso-diametric parenchyma cells which make up the cotyledons. Vascular bundles run through the cotyledons and the embryonic axis, and intercellular air spaces occur. Starch grains, protein, and sugars in solution, together with tannin and oil droplets fill the cells. Oil droplets are particularly numerous in *Erythrobalanus* and other fatty acorns, and it is possible that textural or other features related to differences between starchy and fatty acorns might be distinguishable in the cotyledons.

5.3. THE ACORN AS A SEED

5.3.1. The acorn as dispersal unit

The primary function of the acorn is to act as an agent of dissemination for the oak, and to produce another oak tree, preferably at some distance from the parent tree, or at least beyond the canopy (oaks are generally relatively intolerant of shade). The life of the acorn as an agent of dispersal, up to and beyond the stage of germination, has been examined by foresters and others, the two most notable studies being those of Watt (1919) and Korstian (1927). Many acorns fall to the ground in autumn, or are removed from the trees or the ground by animals, principally birds and squirrels. Acorns which are not eaten immediately may be dropped, or buried in the ground. If they are not subsequently retrieved, and avoid other perils such as desiccation, often by becoming buried beneath falling leaves, they may germinate when conditions are suitable. Even some partly eaten acorns, as well as those removed from trees before they ripen, are capable of germination (see e.g., Hadfield 1974).

5.3.2. Acorn physiology

Certain physiological characteristics may be important in relation to the ways in which acorns can be used. In particular, those physiological characteristics which relate to their persistence as an overwintering disseminule might have an important bearing on their ability to be used a storable food resource.

5.3.3. Dormancy and germination

Some acorns, including those of the white oak group (Griffin 1971; Korstian 1927), have no inherent seed dormancy, and occasionally even begin to germinate while still on the tree (Jones 1959; Korstian 1927). In Britain, acorns of *Q. petraea* germinate particularly promptly, while for *Q. robur* there is a longer delay, though members of both species may remain dormant until the spring. Acorns of the North American red oak group do not generally germinate until the following spring, though Baldwin (1942) reports *Q. rubra* acorns germinating in autumn. Experiments with some members of the red oak group have shown that, although there is apparently no overwintering or vernalisation requirement, the acorns do possess a certain amount of inherent dormancy, and must undergo a certain amount of after-ripening before they will germinate (Griffin 1971; Korstian 1927). The potential significance of such factors are discussed further in 6.2.2.2. and 6.4.1.

5.3.4. Moisture content

Acorns, together with many other large temperate-forest tree seeds, are recalcitrant seeds - they rapidly lose viability when they become dry (Gosling 1989). Red oak acorns are generally able to lose a greater percentage of their water before they lose their viability, and it has been suggested that this relates to their generally higher fat content (Korstian 1927). Table 12 indicates some of the estimates that have been made for water content at time of collection for acorns of different species. Because water loss can occur so rapidly it is difficult to make comparisons between figures, but those studies that specifically approached this question concluded that total water content seems to be greater in acorns of the white than those of the red oak groups (Burns and Viers 1973; Goodrum *et al.* 1971; Korstian 1927) and this is generally supported by the figures presented in Tables 8 and 12. Gaussen and Rouquette (1949) examined moisture content in acorns of two North American red oaks and seven European white oaks. The American oaks were lowest in moisture, followed by *Q. coccifera*, *Q. ilex* and *Q. suber*, and then the deciduous oaks. They found moisture content to vary within species, apparently in relation to climatic influences, growing conditions and conditions at time of collection.

5.3.5. The acorn as a large seed

One characteristic that makes acorns a potentially attractive food, to people or other animals, is their relatively large size, and this relates to the particular way in which they achieve their role of dissemination. Large seed size is generally a characteristic of species which germinate in conditions of heavy competition, shade, or drought, and seems to relate to prompt germination, increased vigour, and greater survival in seedlings (Fenner 1985; Irgens-Moller 1955; Salisbury 1942; von Teichmann and van Wyk 1991). Observations by various workers cited by Baldwin (1942), Salisbury (1942) and Korstian (1927), as well as experiments undertaken by the latter, and by Tripathi and Khan (1990), have demonstrated that even within populations of acorns, the larger ones germinate more rapidly and produce larger seedlings, though any benefit is not necessarily carried over into later life.

Apart from providing a reserve which can be drawn upon for a considerable time after germination, and which enables the shoot to emerge into the light when buried at some depth, as many animal-dispersed acorns are (Fenner 1985), large seed size may have other benefits. It may reduce the likelihood of injury from external conditions, such as frost or desiccation, to which acorns are particularly vulnerable. Von Teichmann and van Wyk (1991) however, suggest that large seed size is a disadvantage in water relations. The major drawbacks of large seed size are thought to be the lesser ease of dispersal, the greater risk

of predation, and the greater allocation of reproductive effort invested in individual seeds (which often means that large seeds are produced in (relatively) small numbers) (Fenner 1985; Salisbury 1942; von Teichmann and van Wyk 1991). Tripathi and Khan (1990) however, found that in two relatively small-seeded acorns it was the light and medium weight seeds which suffered greater risk of predation, and they suggested that the production of large quantities of these smaller acorns might protect the larger, more competitive, ones from predation. Jones (1959) has also noted that trees will tend to produce large numbers of small acorns together with the more normal sized ones. Whatever the ultimate benefits or disadvantages of large size, acorns provide a bulk supply of energy for the germinating seedling, or, alternatively, for any predator which can utilise it.

5.3.5.1. Variations in acorn size

Acorn size varies considerably within the genus, and may be an important consideration in human use. For example, in North America, acorns of *Q. macrocarpa* may be 5cm long, and weigh 30-40g when fresh, and some Mexican and Colombian species are of similar, or possibly greater, size; while many other species may be tiny and weigh much less than a gram (Kaul 1985; Miller and Lamb 1985; Smith 1929). In theory acorns which store much of their energy as fat (such as the red oak group - see 6.2.2) should tend to be smaller than those which store enery as carbohydrate, as fat enables a larger quantity of energy to be packed into a smaller volume (Slack and Browse 1984), but this relationship is not proven in oaks (see Table 12). Waller (1979) notes that seed size in general is larger in trees which have a mast interval (as the oaks do - see Appendix3) compared with those which exhibit regular annual production, but this relationship is again untested within the oaks.

Muller (1951) commented on the superficial nature of acorn size as a taxonomic character, and noted that it was very variable, especially with hybridization (see also Brookes and Wigston 1979). Schreiner and Duffield (1942, cited in Irgens-Moller 1955) found that hybrid *Q. alba*/*Q. robur* acorns were larger than those from selfed populations; while Brookes and Wigston (1979) found that hybrid acorns were smaller.

Seed size certainly may vary considerably both within species, and among acorns on the same tree (see, for example, Brookes and Wigston 1979). Jones (1959) comments that the apical acorns in an inflorescence usually remain smaller than the lower acorns, though even those as small as 0.5g are viable. Variations in seed size may also be considerable from year to year, as indicated in Appendix 3, 3.3.

Gaussen and Rouquette (1949) examined acorn weights from several populations of seven native and two North American species in France. Although they found that average

weights of *Q. ilex* and *Q. coccifera* were less than for the other species, variation within species was greater than any between species. There did not appear to be any consistent regional basis for weight variation. Samples of *Q. pubescens* collected in one year within one forest had a greater range in weight than other populations of all species combined. They suggested that factors such as the age of trees, and local environmental factors favouring or reducing growth, were more important than either inter-specific or regional variations.

Shell thickness can be an important component of acorn size (see Table 12). Gaussen and Rouquette found that this did seem to vary consistently on both a specific and a regional basis. The highest shell contribution to total acorn weight for the European species was consistently found in *Q. coccifera*, with the lowest in *Q. ilex* and *Q. suber*. There was, however, a significantly smaller proportion of shell in all these species than in the two North American species, in which shells comprised almost a third of the total acorn. Within all species there was a tendency towards a smaller proportion of shell in warmer areas.

CHAPTER 6. THE ACORN AS A FOOD RESOURCE - NUTRITIONAL AND BIOCHEMICAL CHARACTERISTICS

6.1. INTRODUCTION

The nutritional characteristics of acorns are undoubtedly of great importance in relation to their use by people as a food resource. This chapter presents the available data on these nutritional characteristics. The role of tannins, and of other factors which may affect the taste or "edibility" of acorns, is also discussed.

6.2. THE NUTRITIONAL CONTENT OF ACORNS

In comparison with other 'nuts', acorns are generally included among the starchy seeds, along with chestnuts, in comparison with, for example, the hickories, high in fat, or the walnuts and beech, high in protein (Baldwin 1942). These categories are very much generalisations (some beech, for example *Fagus sylvatica*, as Baldwin notes, may contain 42.9% oil). Table 7 provides a general comparison of nutritional components of some temperate forest nuts.

Table 8 shows the results of nutritional analyses which have been undertaken on acorns. There are various problems with comparability of the data included in the table, which are discussed further in Chapter 7. Notwithstanding these potential problems in comparing results of different analyses it was thought that an attempt to compare the data for different oak groups, and for regions, on a very gross basis might be of interest. Table 9 gives comparisons of the major nutrients, Table 10 on tannin content. Table 11 summarises data on energy values of acorns, and is discussed further in Chapter 7. In cases where it was felt that the data were insufficient no averages are shown for a particular region.

Table 9 was calculated from a sub-set of the data included in Table 8, excluding all figures which were for processed acorns (as flour, leached acorns, bread, etc.) as well as those for which the total of all constituents did not approximate 100% (because of insufficient data in the source reference). In the case of the East Asian region there were few samples, of which only half had totals equalling 100%, and which included samples with anomalously high fat values. In this case it was not possible to produce a table of averages. For the first three regions comparisons were made between samples analysed with and without shells, and only in the case of the eastern North American acorns were consistent differences apparent, as shown by Table 9. In the other regions such differences were not apparent, probably because of biases introduced due to the considerably smaller numbers of samples.

Table 10 includes the averages of all samples in Table 8 where tannin values have been given, excluding Europe, where insufficient analyses were present. In all cases analyses were undertaken on acorns without shells.

As the tables indicate there are some potentially significant differences between species. The most obvious of these are in the quantities of fat and carbohydrate, which may vary considerably between species, sometimes in relation to taxonomic divisions, most notably between the red and white oak groups in North America. Some of the most significant differences in seperate components are discussed in the following sections, and there is further discussion of intra-specific variability in nutritional components in 6.4.

6.2.1. Protein

Acorns are low in proteins in relation to many other foods, notably many other nuts (see Table 7). In animal feeding studies acorns are generally considered a poor source of protein (see Appendix 4, 4.4.6.7.1.). In addition, much of the protein present may be unavailable because of tannins in the acorns (see Apppendix 2, 2.4.2). A few studies have examined in more detail the types of proteins and amino acids present in acorns (Bainbridge 1987; Lund and Sandstrom 1943; Taleb-Bendiab *et al.* 1990), and the make-up of the protein of *Q. ilex* was noted in one study to be closer to that of wheat and maize than to peas and soya.

Averages from Table 9 do not indicate any consistent differences in protein values between the different regions or taxonomic categories. Gaussen and Rouquette's (1949) study indicated differences in protein content between some species, with *Q. coccifera*, *Q. ilex* and *Q. pubescens* noticeably lower in this constituent than acorns of the four other European and two North American species. Petrucci's (1947) study of four species in Italy found that *Q. petraea* appeared to have significantly greater protein content than *Q. robur*, *Q. ilex*, and *Q. cerris*. An examination of the data inTable 8 for species for which there are several samples provides some support for the suggestion that there may sometimes be consistent differences between species, irrespective of taxonomic groups. For example, in eastern North America, compare *Q. ilicifolia* with *Q. nigra*, or, in Europe *Q. cerris*, *Q. petraea* and *Q. robur* with *Q. brantii* and *Q. coccifera.*

6.2.2. Fats

6.2.2.1. Fat content of acorns

As is evident from Table 8 variation between species in fat content in acorns is particularly marked. The averaged data for North America given in Table 9 shows that fat content in

acorns of the red oak group is significantly greater than that of the white oaks, with an average value in both the eastern and western samples around three times higher. Because of the presence of this group the total average fat values for North American acorns are more than twice as high as the total for European acorns. Variations in fat content between acorns in other parts of the world apparear less extreme. Data in Table 9 for Europe suggests that both the *Cerris* and *Ilex* groups appear to be slightly higher in fat than the *Quercus* group, but the ranges of the groups overlap. It appears that there may also be consistent differences between individual species within regions or taxonomic groupings - compare *Q. ilex* (Table 8) with all others, though note the comparably high fat values in some samples of *Q. brantii.* In Gaussen and Rouquette's study, referred to above, lipid values in the European species studied were all similar, with only*Q. ilex* having significantly higher values than the others. A study of several populations in Spain confirmed the relatively high proportion of lipids in this species (Mazuelos Vela *et al.* 1961), though Petrucci's (1947) study gave much lower lipid values for samples collected in Italy.

Some studies have examined the composition of oils extracted from acorns in more detail, usually from those species high in fat, some of which have been considered as potential commercial oil sources, and the oil has been compared favourably with olive oil (Bainbridge 1987; Khan *et al.* 1977; Mazuelos Vela *et al.* 1961; Puntambekar and Varma 1934; Smith 1929; Wolf 1945).

6.2.2.2. Causes and correlations of variation in fat content of acorns

Because fat content is one of the more variable elements of acorn nutrient content, and because the role of fats in human diets has been of some interest in studies of past human subsistence (e.g., Harris 1981; Speth 1987), the possible correlates and causes of their presence in acorns is considered further.

Korstian (1927) suggested that the high fat content of red oak acorns is correlated with their dormancy requirement. The acorns need to go through a process of after-ripening, when fats are converted to soluble carbohydrates, before they can begin germination. After-ripening in acorns occurs naturally in temperate regions when the acorn falls and is covered by leaves, and sometimes snow, where it remains damp and cool until the following spring (Crocker and Barton 1953).

Korstian compared chemical analyses of fresh acorns, and of those stored (as viable seed) until the following April, and found considerable reductions in fat between the two measurements, with corresponding increases in carbohydrate. These differences were

greater in the white oaks than the red oaks, probably because the germination process in spring was more advanced in white oaks. Korstian also noted that one white oak, *Q. bicolor*, and the European *Q. cerris*, both of which show some germination delay, had fat levels intermediate between those of other white oaks and the red oaks. Korstian further suggested that acorns high in fats may be delayed in their germination, relative to carbohydrate-storers, because of the greater energy requirement for hydrolysis of fat, and the consequent need for higher spring temperatures.

In contrast to Korstian's study, nutritional analyses undertaken by King and McClure (1944) indicated an increase in percentage of lipids in a germinating sample of *Q. nigra* acorns (see Table 8). This finding however, contradicts much of what is known of changes in storage reserves during germination. Investigations of after-ripening in acorns have provided more details on the chemical changes they may undergo after they have fallen from the trees. Experiments by Brown (1939, cited in Crocker and Barton 1953), showed that under after-ripening conditions (cold, moist storage) acorns of *Q. rubra* and *Q. alba* convert oils to soluble sugars, and then, on germination, lower oxygen substrates - carbohydrates, are formed.

The likely correlation of fat content with dormancy requirement in acorns is supported by general findings regarding seeds whose major storage reserves are carbohydrates rather than fats. Baldwin (1942) comments that, within tree seeds as a whole, those rich in carbohydrate are not generally designed to withstand physiological or other drought, and large seeds especially which store their reserves as starch tend to germinate quickly.

The possible correlation of fat content with dormancy is particularly interesting because the high-fat red oak acorns also tend to be high in tannins. As noted in Appendix 2, the presence of tannins is also thought to be correlated with dormancy in seeds.

6.2.3. Carbohydrate

Acorns are relatively high in carbohydrate, though with recorded values ranging from around 50% to over 90%, and averages for four regions from around 60% to over 80% (see Table 9, for samples without shells) they are more variable, and often lower, in this constituent than are the principal carbohydrate sources of modern diet, the cereals and rootcrops - as a percentage of dry weight values for carbohydrate content of wheats, barley, rye sorghum, millet, rice, maize, potatoes and yam given by Watt and Merrill (1963) all fall between 80 and 90%.

The carbohydrate content of acorns is particularly low in acorns with high fat content, notably those of the North American red oak group, as Table 9 illustrates. European acorns, of all taxonomic divisions, appear relatively high in carbohydrate, which may partially reflect their generally low fat content. However, this is the case even in comparison with the low-fat American *Lepidobalanus* group.

Gaussen and Rouquette (1949) examined variation in nutritional components of seven native and two North American (red oak group) species growing in France. Total carbohydrate varied little between the European species, but was markedly lower in the two North American species. Gaussen and Rouquette also looked at the relative contribution to total carbohydrate of starch and sugars. Highest sugar and lowest starch was found in acorns of the evergreen *Q. coccifera*, *Q. ilex* and *Q. suber*, and acorns of the deciduous *Q. pubescens* were also relatively high in sugar. There were generally lower quantities of sugar in acorns of the other deciduous oaks. The potential significance of sugars in acorns is discussed further below (see 6.5).

6.2.4. Vitamins

Some studies have reported acorns to be high in certain vitamins or vitamin groups. King and Titus (1943, cited in King and McClure 1944) found acorns of *Q. phellos* to be high in Vitamin A. Other studies, (see Bainbridge 1987; Bainbridge and Felger 1989) have found raw acorns to be a good source of Vitamin C, and some species to be high in some of the B group vitamins. Kuzayli *et al.* (1966) presents data on some vitamins in an unspecified Lebanese species.

6.2.5. Minerals

Several studies have reported the quantities of minerals present in some acorns, including Baldwin (1942), Beck and Beck (1955), Bonner (1971, 1974), King and McClure (1944), Kuzayli *et al.* (1966), Landers *et al.* (1977, 1979), Papp (1985b), Scrivner *et al.* (1988), Torgerson and Pfander (1971), Short (1976), Short and Epps (1976), Wagnon (1946, cited in Duncan and Clawson 1980), and Wainio and Forbes (1941). Wainio and Forbes commented that, in comparison with wild fruits from the same area (Pennsylvania), all nut species were low in calcium and phosphorous, with acorns among those particularly low in calcium. Short and Epps (1976) found acorns to be lower than other squirrel foods in phosphorous. Havera and Smith (1979) examined nut foods eaten by squirrels and found all to be low in calcium and sodium. Calcium was especially variable between oak species. Menke and Fry (1980) carried out one of the few studies to examine seasonal changes in mineral content over the period of growth of acorns. They found little significant variation

in the concentration of nitrogen and phosphorous over time, compared with the variation in these elements in leaves. Brookes and Wigston (1979) examined variation in mineral content of acorns within and between *Q. petraea.* and *Q. robur*, and found the most significant variation to correlate with size of the acorn. With increasing acorn size total mineral content increased, though this was more consistent in the case of potassium, in which both species were high, than in calcium and sodium. As a proportion of dry weight, however, nutrient content decreased with increasing size, and this was more marked in the usually smaller acorns of *Q. petraea.*

6.3. TANNINS IN ACORNS

Acorns contain tannins to a varying degree, which need to be removed by processing of some kind before they become palatable. The extent to which tannins might have harmful effects on people, or on animals eating acorns, and the way in which they produce their astringent effect, together with a brief discussion of their role in plant tissues, is presented in Appendix 2.

The precise nutritional effects of the different tannins, or polyphenols, either as protein binders or as enzyme inhibitors, is a complex field of study, and to what extent different tannins are present in acorns of different species is virtually unknown. The quantities of tannins which would need to be consumed before any harmful effects were felt is also uncertain, especially for humans, though feeding studies and observations have been made with several vertebrates. Although the taste of all but the sweetest untreated acorns is often reported to be repulsive, as Harborne (1982) points out, it is possible for animals, including humans, to develop a taste for the astringency of tannins; and it is also possible that there may be genetic variation in the perception of the astringency of tannins.

Very few quantitative analyses of tannins in acorns have been undertaken, as Tables 8 and 10 show, and it is difficult to come to any conclusions about variations in this component. Analyses of acorns of *Q. alba* and *Q. prinus* from two sites in the American Northeast showed that tannin concentrations were greater in both cases in samples collected in North Carolina than in Connecticut (Korstian 1927). The potential effects of environmental conditions on quantities of tannins in acorns is uncertain. Tannin content in leaves has been found to increase in trees of some species growing on low nutrient soils (Harborne 1982). North (1967) notes that the toxicity of acorns to cattle seems to vary from year to year depending on weather conditions.

The figures shown in Table 10 provide some support for the proposition that tannin concentrations are greater in red oaks than in white oaks, but only by a small margin, and

with overlapping ranges. A similar situation occurs in Japan, where analyses suggest that acorns of the *Cyclobalanopsis* sub-genus are lower in tannin than members of the *Quercus* sub-genus. The highest value recorded for the *Cyclobalanopsis* group is for an Indian species, *Q. leucotrichophora*, which overlaps with figures recorded for acorns of Japanese members of the *Quercus* sub-genus. This species is, in fact, included in *Quercus* by Camus (1936-1954), but has subsequently been moved to *Cyclobalanopsis* (Kaul 1985).

General problems with tannin analyses (discussed in Appendix 2 and Chapter 7), together with those presented by the small numbers of analyses undertaken, mean that the averaged figures shown in Table 10 may be relatively meaningless. However, where figures for different taxonomic groups are presented in individual sources those for *Erythrobalanus* are consistently higher than those for *Lepidobalanus* (Koenig and Heck 1988; Servello and Kirkpatrick 1989; Wainio and Forbes 1941; though others do not indicate clear differences - Korstian 1927; Wagnon 1946, cited in Duncan and Clawson 1980), and in Japan values for sub-genus *Quercus* are all higher than those for *Cyclobalanopsis* acorns.

Figures shown in Table 8 for the few species for which several analyses have been undertaken suggest that there may be considerable intra-specific variability in tannin concentration, though again, there are no secure data on this. There may also be consistent differences between species irrespective of taxonomic group. For example, figures for tannins in acorns of *Q. prinus* shown in Table 8 are consistently high in relation to figures for other members of *Lepidobalanus* for which several analyses have been undertaken.

The fact that many ethnographic studies emphasise the importance of removing the testa of acorns, suggests the likelihood that tannins are present in strong concentration here. The relative astringency of the testas of sweet chestnuts is well-known, and tannins are known to be concentrated in the testas of some leguminous seeds (e.g., Elias *et al.* 1979; Vaillancourt *et al.* 1986). Analysis of some of the components of acorns by Trimble, shown in Table 5 suggest that this may be true of acorns. Other analyses shown in the table, undertaken by Korstian (1927), indicate some of the potential variability between cotyledons and pericarps in relative tannin concentrations. In the white oaks the percentage of tannins was found to be greater in the pericarp than in the embryo, while in the red oaks tannin concentrations in pericarps were found to be far smaller than in the embryos. It is possible that there may be similar degrees of variability in tannin concentration in testas, but there are no data on this.

Species	Tannin Concentration (% dry weight)			Source
	Cotyledons	Testa	Pericarp	
Lepidobalanus				
Q. alba	7.8	—	12.5	Korstian 1927
"	4.4	—	6.5	"
Q. prinus	8.9	—	11.0	Korstian 1927
"	7.8	—	8.3	"
"	8.8	42.1	16.0	Trimble 1896
Erythrobalanus				
Q. rubra	7.4	—	1.7	Korstian 1927

Table 5. Comparison of tannin concentrations in acorn components

The potential significance of variations in tannins in acorns is discussed further in 6.5.

6.4. VARIATIONS IN BIOCHEMICAL COMPONENTS OF ACORNS

There is great intra-specific variability in many oak characteristics (see 4.3.4. and Appendix 3). This seems likely to be as true of acorn nutritional qualities as it is of other characteristics, and may relate to genetic factors, to the local environment, or to particular climatic and other environmental conditions prevailing in the year of production. The figures shown in Table 8 give some indication of the potential intra-specific differences, though all values given are not necessarily truly comparable (see Chapter 7). Very little work has examined systematically or in great detail variability in nutritional components within species of oak. However, some of those studies which have explicitly examined intra-specific variability in nutritional components are discussed below.

King and McClure (1944) summarised some of the environmental factors which had been found to influence nutritional content of wild plants being used as animal feed. They included soil type and period of exposure to the weather, with loss of nutrients over time. They looked at the nutritional content of acorns from different populations of several species. Their figures (given in Table 8) show that there were sometimes quite large differences in nutritional components between samples. In particular fat and carbohydrate values varied within *Q. marilandica* and *Q. michauxii* by up to 10%, while in *Q. nigra*, *Q. stellata* and *Q. phellos* they varied within less than 5% in this component. These analyses included the acorn shell, differences in the quantity or thickness of which could potentially introduce significant variation into the analyses. However, in the species in which there were large differences, the lower fat analyses are accompanied by corresponding increases

in carbohydrate, rather than changes in fibre content which would be most likely to reflect differences in contribution of the shell. In *Q. michauxii* the decreased fat level was also accompanied by almost a doubling in protein content. In this species it is possible that some of the differences were due to varying extents of ripeness of the samples (see 6.2.2. and 6.4.1.), though they were also from different sites. The small differences in fat content found in the other species were accompanied by a combination of small differences in protein, carbohydrate and fibre.

In Gaussen and Rouquette's (1949) examination of differences in nutritional content between populations of oak species in France they considered in particular the possibility of regular differences related to the region of collection. Quantities of ash within species appeared to show a general decrease as samples approached the Mediterranean climatic zone. However, no consistent regional variations in lipids, proteins, or carbohydrates were apparent. For all nutritional components and species considered together there were only weak variations attributable to the region of collection of samples.

A study of *Q. ilex* acorns in Algeria discovered both regional and altitudinal differences in some of the amino acids present (Taleb-Bendiab *et al.* 1990). Another study of this species in Spain found little variation between eight populations in any constituent (Mazuelos Vela *et al* 1961). Nutritional analyses reported by Wolf (1945) showed great variation in lipid quantities in acorns of *Q. agrifolia*, between different subspecies, populations and areas.

Gysel (1957) compared samples of acorns collected from sites of differing quality for growing oaks, classed as good, medium and poor. Combinations of three different species were present on the three sites, so it is difficult to draw conclusions about the possible effects of site quality. In *Q. alba*, for instance, protein and lipids were higher in samples from the medium site than the good site, while in *Q. velutina* they were higher in the medium than the poor sites. Carbohydrate values occupied the reverse positions.

Tripathi and Khan (1990) examined differences in nutritional value of acorns collected from the same trees and grouped into different size classes. They found fat content generally higher in the bigger acorns, largely at the expense of lower carbohydrate values (see Table 8).

Petrucci (1947) examined differences between acorns produced in a year of good production and the following year of poor production, for four Italian species, but found differences in nutritional components between the two years were very small.

6.4.1. Variations in nutritional composition of acorns depending on time of harvest or storage period

Acorns may vary in their nutritional value in relation to the extent of their maturity or ripeness, or to physiological changes undergone after they fall or are removed from the trees. While they remain alive they may undergo biochemical changes. Some of those relating to the effects on lipids of after-ripening, dormancy and germination have been discussed in 6.2.2. Other studies have indicated other potential changes.

Gaussen and Rouquette (1949) suggested that some of the inter- and intra-specific variation which they found in the proportions of sugar to starch was due to the fact that some of their samples had begun to germinate. Hydrolysis of carbohydrates had occurred in these samples, so that the proportions of sugar to starch were greater. Germination may have other effects on the nutritional value of acorns. Smith and Follmer (1972) discussed the adverse effect on the assimilation rate of acorns by squirrels of the development of radicles, containing indigestible structural and vascular tissue of cellulose and lignin, during germination. They observed squirrels discarding the radicles and adjacent tissue. Wood (1938) also noted squirrels biting the tips off acorns and rejecting them. Davison (1964) examined squirrels' preferences for acorns of *Q. palustris* collected in each month from September to December, and found no differences. As members of the red oak group these acorns should not have begun to germinate, but their might be differences between months relating to after-ripening, or to leaching of tannins in those which had been on the ground longest.

"Green" or immature acorns are often said to be more astringent, or more damaging to livestock (Cooper and Johnson 1984). Smith and Follmer (1972) compared the effects on squirrels of eating almost mature acorns, picked from the trees, with those which fell to the ground within the following two weeks, and found no significant differences. However, they found that very immature nuts, picked around a month earlier than ripe acorns were largely rejected by squirrels. They also commented on the considerably smaller size of acorns picked from the trees only four days before apparently mature acorns were picked, suggesting that there may be rather rapid changes in the period just before maturation. There are, however, few studies detailing the biochemical changes undergone in acorns during the ripening period. King and McClure (1944) included two samples of *Q. michauxii* in their analyses, one of which was collected in September, the other during "Fall". The first was considerably lower in fat, and relatively higher in protein and carbohydrate, while the latter was high in fat and lower in protein and carbohydrate. Unfortunately, these samples were collected from different trees in different sites, so other factors than the degree of ripeness of the acorns might account for this variation.

6.5. SWEETNESS AND "EDIBILITY" OF ACORNS

The taste of acorns may be a significant factor in their use by people. Acorn flavour varies considerably, and some may have a taste resembling chestnuts, cashews, or chocolate (Bainbridge 1987; personal observation). One of the most significant taste characteristics is the extent of "bitterness", or more strictly, astringency, of acorns, which largely relates to tannin content. As noted in 6.3 few quantitative analyses of tannin in acorns have been performed. In North America acorns of *Erythrobalanus* are generally said to be bitter, and those of *Lepidobalanus* sweet (e.g., Fernald and Kinsey 1958; McPherson and McPherson 1977; Morris 1927; Preston 1961; Smith 1929).

Much of the reference to astringency or otherwise of acorns is apocryphal and non-quantitative. For instance, the extent of "sweetness" within the North American white oak acorns is relative, and within the group there are apparently differences. Some of the species which have been particularly noted for their sweetness or "edibility" include *Q. douglasii*, *Q. gambelii*, *Q. garryana*, *Q. havardii*, *Q. lobata*, *Q. michauxii* ("sweet and edible" - Downs 1949), *Q. muehlenbergii* ("sweet and sometimes edible" - Morris 1927), *Q. prinoides*, *Q. prinus*, *Q. stellata*, *Q. undulata* and *Q. virginiana* (Hedrick 1972; McPherson and McPherson 1977; Miller and Lamb 1985; Morris 1927; Sargent 1905; Smith 1929; Van Dersal 1940; Wolf 1945).

Some members of *Lepidobalanus* are recorded as possessing "bitter" acorns, including *Q. oblongifolia* (Smith 1929) and *Q. arizonica* (Sargent 1905), though Preston (1961) records this species as sweet.

One species of the *Erythrobalanus* group that has been frequently recorded as sweet is *Q. emoryi* (Hedrick 1972; Miller and Lamb 1985; Preston 1961; Smith 1929), and Morris (1927) cites examples of some trees of *Q. agrifolia* (otherwise usually recorded as "bitter") which were sweet enough to be eaten raw. Interestingly, both these species are unusual within the red oak group in maturing acorns within only one season.

In the Old World too, some acorns are reputed to be sweet, including *Q. ilex* (Gaussen and Rouquette 1949; Hedrick 1972; Morris 1927; Parsons 1962; Smith 1929), though in some cases this sweetness is only said to develop after a period of storage (Howes 1948; Loudon 1907, cited in Smith 1929). Both the Flora of Turkey (Hedge and Yaltirik 1982) and Flora Europaea (Tutin *et al.* 1964) however, note that *Q. ilex* has "bitter" fruits, and distinguish *Q. rotundifolia* in Southwest Europe, and *Q. aucheri* of southwestern Turkey and the islands, both of which have been included within *Q. ilex* , as the sweet species. Another "sweet and edible" species is *Q. ithaburensis* ssp. *macrolepis* (Smith 1929). Other species

are not generally so sweet, including *Q. robur* and *Q. petraea* (see, e.g., Howes 1948) though individual trees of *Q. petraea* have been noted to bear sweet acorns (Morris 1927), and Burkill (1935) commented that within the British oaks (which he classed as one species) is a variety with sweet acorns, contrasting with the usual "bitter" types. Corbet (1974) notes that there is known to be great variation in both sugar and tannin content in acorns of both *Q. petraea* and *Q. robur*. Acorns of the relatively sweet *Q. brantii* also vary somewhat in their sweetness (personal observation), but it is uncertain in many of these cases whether these differences are consistent for acorns of any one tree from year to year.

One problem with attempting to determine from the literature whether nuts are sweet or not is that in many cases it is uncertain whether a reference to edibility means that the acorns are not astringent - in some cases they certainly are. Even if more information on tannin content was available, not all sweetness can be explained by the quantities of tannins present. Gaussen and Rouquette (1949) carried out nutritional analyses of many oak species in France and noted that the relative quantities of starch and sugars making up the carbohydrate values varied between certain species. Acorns of *Q. coccifera* had the highest sugar content, but nevertheless tasted "bitter", presumably because of a high tannin concentration. They found that acorns of *Q. ilex* and *Q. suber*, despite having lower sugar concentrations, were noticeably sweet. It is possible that the apparent anomaly of the high recorded tannin values for *Q. prinus* with the frequently recorded "sweetness" of acorns of this species noted above may be due to similar factors. Few nutritional analyses of acorns provide any information on this, though Korstian (1927) presents figures suggesting that there may be variation in sugars between members of the red and white oak groups, with the former group lower in sugar. He suggested that high fat and high sugar values were negatively correlated. In Gaussen and Rouquette's study, however, which involved seven relatively low fat European species and two North American *Erythrobalanus* species, the acorns lowest in fat were also lowest in sugar.

Neither tannin nor sugar concentrations alone necessarily determine the sweetness or astringency of acorns, and there are insufficient data available on either of these factors to suggest whether there might be correlations, positive or negative, between them. The paucity of quantitative data on either sugars or tannins in the acorn literature means also that it is difficult to say to what extent these two factors might be involved in human preference for different species. The confused picture presented by the nutritional data with regard to sweetness/bitterness of acorns means that ethnographic literature indicating use of one or other type of acorn should perhaps be interpreted with greater caution than is usually applied.

CHAPTER 7. BIOLOGICAL DATA ON THE ACORN RESOURCE - SUMMARY AND DISCUSSION OF PROBLEMS

7.1. INTRODUCTION

Models of the potential for use of food resources in the past, as indicated in Chapter 2, generally have two main requirements. These are the requirement to make quantitative (or at least relative qualitative) estimates of available yields (often in nutritional terms), and the requirement to be able to accurately characterise the "behaviour" of the resource.

Some of the physiological characteristics which constitute part of acorn "behaviour" have been described in Chapter 5, and nutritional and biochemical characteristics have been discussed in Chapter 6. A great deal of information exists regarding the production of acorns, and the well known periodicity or masting behaviour of oaks. In addition a considerable number of studies have attempted to measure the yields of acorns, of individual trees, of species, or of several species in a given area. In Appendix 3, the literature on the factors affecting acorn production is discussed, and quantitative data on yields are presented in Appendix 3, Tables 12-15. A further factor of importance in relation to the use of acorns by people is the extent to which the potential crop is available, and to what extent it may be damaged or destroyed by insects or vertebrate competitors. The available literature on this topic is summarised in Appendix 4, and quantitative data on potential losses from the acorn crop are presented in Appendix 4, Table 16. In this chapter the conclusions which can be made about potential acorn yields, losses, and "nutritional yields", are summarised, and problems associated with using the available data in resource modelling are discussed.

The two major components usually included in quantitative models of resource use are yields and nutritional value. The first of these requires consideration in terms of both quantities available and timing of availability; the second in terms of quantities, food quality, and perhaps complementarity with other food sources. Estimates of nutritional yield (in terms of energy value, macronutrients, or micronutrients) involve both components.

7.2. YIELDS

7.2.1. Data on yields

A considerable amount of data exists on the quantities of acorns produced by different species of oak and in different areas, though much of it relates to North America. Most information comes from studies carried out by foresters and wildlife biologists largely within the last 70 years.

An attempt has been made to summarise much of the published information in Tables 12-15. Data relevant to yields have been expressed in several ways in the literature, and the individual tables each cover a different type of yield estimate. In some cases information of each type is available in one source, in many it is not. In some cases only average estimates are presented, in others averages have been calculated from the available data, and in many cases converted to standard units to facilitate comparison. However, within the categories of information the nature of data provided by different sources varies, and it has not always been possible to present all the information in directly comparable forms.

Table 12 shows estimates given for the average weight of individual acorns. As the table indicates, in some cases direct measurements of individual acorns exist, so that it has been possible to present the range of weights within a sample. In some cases averages for different years or individual trees have been made, and again it has been possible to indicate the range of values. In most cases only one average figure exists, though this may have been derived from anything from one individual in one year to an average of many over several years.

Most available yield data relate to estimates of the weight of acorns produced by individual trees in any one year, and again, depending on the nature of the data it has been possible to present a combination of ranges and averages (Table 13). Where data were presented in terms of numbers of acorns produced per tree average weights of acorns determined by the same study have been used to produce a yield figure in terms of kg/tree, though, unfortunately, in many cases this was not possible.

In some studies estimates of production per unit area by individual species were given, and again in some cases figures given in terms of acorn numbers have been converted to give a measure of yield in kg per unit area (Table 14).

Finally, in some cases where several species were included in the same study area, or where large tracts of individual species cover large areas, figures of total yield have been

given. Where they were not, but individual yields of several species were given, these have been combined to produce an estimate of total acorn yield per unit area, in an attempt to provide some basis for regional comparison (Table 15).

The intention in compiling the tables has been to provide some basis for comparison of species and regions, though as is apparent from the following discussion the extent to which there is true comparability between data from various sources is highly questionable. However, treated with caution, the tables give some idea of the wide ranges in variation of different measures of yield, within and between individuals, species and years, both between and within individual studies.

7.2.2. Measurements of acorn yields

Acorn yields presented in the literature are sometimes expressed on a qualitative comparative basis, and sometimes quantitatively. Various methods of determining acorn yields, and in many cases discussions of problems encountered in doing so, have been described by the following: Allen and McGinley (1947), Burns *et al.* (1954), Christisen (1951, 1955), Cypert and Webster (1948), Dalke (1953), Downs (1944), Feret *et al.* (1982), Goodrum *et al.* (1971), Graves (1980), Gysel (1956, 1957, 1958), Koenig (1980), McQuilkin and Musbach (1977), Menke and Fry (1980), Nicholas and White (1984), Nixon *et al.* (1975), Passof *et al.* (1985), Petrides *et al.* (1953), Segelquist and Green (1968), Tryon and Carvell (1962). Not all the studies whose results are included in Tables 12-15 specify the precise methods used to arrive at their estimates. Many more measures of yields than those included in the tables undoubtedly exist, often in unpublished reports, though Nicholas and White (1984) commented that, at least in North America, this is very often data of a qualitative nature, because of the difficulties of accurately measuring yields.

7.2.2.1. Estimating numbers of acorns produced

Methods of estimating acorn yield generally involve first counting acorns on individual trees, often those fallen to the ground and collected in traps. Sometimes counts of acorns are made while they are still on the trees.

Problems with quantitative measurement will vary depending on the precise type of data being gathered, but some which have been acknowledged by those carrying out various studies include the following. Varying results may be produced by different design of acorn trap (Gysel 1956). There may be difficulty determining which tree acorns have come from when they are growing in dense stands, and when smaller acorns are blown from the

tree by winds (Allen and McGinley 1947; McQuilkin and Musbach 1977). Because of the great individual variation in productivity a relatively large sample is required if it is to include enough trees of similar dimension and position in order to attain a representative average (either for trees of given size classes, or for the population as a whole) (Gysel 1956; McQuilkin and Musbach 1977). In poor years, or for low-producing trees a larger sample size is required (McQuilkin and Musbach 1977). Samples may be biased by removal of acorns from traps or from the ground, and sometimes even by storage of acorns in acorn traps, by squirrels and other animals (Gysel 1956; McQuilkin and Musbach 1977). Another problem is that acorns may be removed by mammals or birds from the trees while still green (Allen and McGinley 1947; Cypert and Webster 1948; Goodrum *et al.* 1971; Tryon and Carvell 1962), so that they never fall to the floor to be counted. The effects of animal predation on acorn yields is discussed in more detail in 7.3. below. Because of removals by animals, especially arboreal feeders, estimates of the numbers of fallen acorns counted should represent a minimum of the potential crop (Goodrum *et al.* 1971; McQuilkin and Musbach 1977).

Counts of acorns while still on the trees avoid some of these problems, but involve other difficulties. Nicholas and White (1984) found that precise timing of counts was essential if accurate figures, comparable between trees or years, were to be obtained. Counting had to be done before any acorns fell or were removed by animals. Another method of estimating numbers is to count the cupules remaining on the ground at the end of the season, which should be representative of the total acorn crop, but if acorns are harvested by animals in the trees before they are fully ripe many of the cupules may well be removed with them and carried off along with the acorn (Gysel 1956; Wood 1938). Some trees may also retain their cupules for a considerable time, making such estimates more difficult.

A further factor which may introduce variability into estimates of yields is the period of time covered by the studies. Both the number of years and the length of time in any season over which counts are made varies between studies. This has been indicated in the tables where information was available.

7.2.2.2. Estimating the weight of acorn yields

Since acorn size is variable both between and within species, counts of the numbers of acorns need to be converted to some measure of weight (Goodrum *et al.* 1971). Although some studies (e.g., Menke and Fry 1980) use direct measures of weight of acorns per trap extrapolated to total weight per tree, many studies begin with counts of acorns and convert these to weights by multiplying by an average often determined from a sub-sample. Because there may be great variation in acorn weight between individuals and years the

most accurate method would be to multiply the number of seeds for each individual in each year by the average weight of the acorns. More often an average weight for the species as a whole, determined over several years will be used (Downs 1944; Goodrum *et al.* 1971; Jones 1959). Some studies use figures derived from other studies, such as, in North America, the average weights given in the Department of Agriculture's "Woody Plant Seed Manuals" (USDA 1974, and its predecessor). These figures are themselves averages derived from varying numbers of studies. Because acorns tend to be bigger than average in good years, and smaller than average in poor years, any multiplication of acorn counts by average figures is likely to bring the extreme yield weights closer to the average.

An example of the problems with quantitative estimates of yields is indicated by some figures given by Jones (1959). He gives the mean weight of *Q. petraea* acorns as 2.5g and of those of *Q. robur* as 3.5g, with the average number of acorns per tree being around 50000. However, the average weight of acorns per tree (presumably measured directly) is given as 16.3kg for *Q. petraea*, and 24.5kg for *Q. robur*. A measure of average yield determined by multiplying average weight of acorns by average number of acorns produced would give values of 125kg per tree for *Q. petraea* and 175kg per tree for *Q. robur*. He also notes the density of acorns on the ground beneath the trees at around 50/m^2, and comments that this is equivalent to 200g/m^2, which suggests an average weight of 4g/acorn. This would give even higher figures for total yield in kg per tree. This example indicates the problems of comparability that there may be between studies which have used different methods to arrive at yield estimates.

Estimates of acorn yield will often include various categories which would be both unusable (as tree seed, or food for wildlife or humans), lighter than sound acorns, such as aborted or sterile acorns, or those partially or wholly destroyed by insects or vertebrates. Other estimates may exclude some of these categories. These differences have been indicated in the tables where they are known; but exact details are not always clear from the literature. In particular, as the figures in Table 16 indicate, the percentage of the total of acorns in the immature category can vary greatly, and in some cases can make up more than 50% of the total crop, or more than 100% of the yield of developed acorns. This potentially large component should be borne in mind when comparing yield figures, as these may or may not include acorns in this category. If an average seed weight is taken from one category and multiplied by a number taken from another category (as may have been the case with the example given above) large inaccuracies may be introduced.

In a few cases figures for yields are expressed in volume measures (litres, quarts or bushels). Such figures are not very useful for comparative purposes, and ideally need to be converted to measures of weight. As the handbook of "Seeds of Woody Plants in the

United States" (USDA 1974) illustrates, however, since acorns vary considerably in size and other characteristics, quite different conversion factors need to be applied to different species (ranging from 14 to 59kg/bushel for the 15 species included in this publication). The potential variation in size and weight of acorns within species in the "Seed Manual" is indicated by ranges in the weight per bushel for one species as great as 35kg. In addition, many of the same difficulties will apply to any such conversions, as for those from acorn count to weight.

7.2.3. Estimating yield per unit area

Resource models are usually concerned with estimates of yield in a given area, and may draw directly upon modern data for similar ecosystems. Since they require consideration of additional factors, such estimates are more complex than those already discussed. The figures presented in Tables 14 and 15 should therefore be treated even more cautiously than those in Tables 12 and 13.

One problem with estimates of yield per unit area given in the literature is that they do not all mean the same thing. Some estimates are made by direct extrapolation of the numbers of acorns per unit area of the tree crown, to provide an estimate of production of individual trees (or perhaps groves of trees) expressed as kg/ha. They take no account of tree density, so that the figures are accurate only for the under-crown areas, or perhaps within a dense stand (which could, nevertheless, be of considerable size), and are not true reflections of the production over a wider area (see Koenig 1980). Alternatively, estimates are made based on the calculated production per tree multiplied by some measure of tree density within the study area (see e.g., Gysel 1957 for a good description of this method). In this case, additional factors which ideally need to be considered include estimates of the numbers of trees of different species present, as well as some estimate of the size and age structure of the population (which may be significant variables - see Appendix 3, 3.3.1.2., and the likelihood of any one tree producing a crop of acorns in any year (see Appendix 3, 3.3.2.2.; 7.2.4.).

Differences between the two methods can be quite substantial. The highest figures for acorn production presented in Table 14, for species in California, are all estimates of the first kind (Bainbridge 1987; Graves 1976, cited in Verner 1980; Menke and Fry 1980). They include several estimates of 2000+ kg/ha, up to 5200kg/ha; while the maximum figures produced by the second method (used by, for example Baumhoff 1981, Bowyer and Bleich 1980; and Wolf 1945), with one exception (see below), are 1175kg/ha (for a crop which was the largest in living memory) and 1568kg/ha (for an area with an extremely heavy crop). In general, the figures presented in the literature from eastern North America

take into account tree densities throughout study areas, while those from California often do not. The highest figure in Table 14 for eastern North America is of a yield, for *Q. alba*, of 1620kg/ha (Johnson 1975), which was apparently calculated by the "California" method. The differences in methodology are possibly partly reflections of the nature of the vegetation in the two areas, with species often mixed through the forests in the east contrasting with more clustered oak groves, often of one species, or oak pasture with widely spaced individual trees in California. It is not always clear which measure of yield is being used in the published reports, and the implications are nowhere discussed explicitly by those making the estimates of acorn yields, probably because most studies are very local and comparisons between different studies are not usually of interest. In at least one discussion of acorn production by a wildlife biologist comparisons are made between the east and California of figures arrived at by the two different methods, with no acknowledgement of these differences (Verner 1980).

One exceptionally high figure for Californian acorn production which does take into account tree density is that estimated by Wolf (1945) for a stand of *Q. douglasii* with 50% tree cover. He estimated that a yield of 5600kg/ha would be reasonable for the better stands in a good season. This would be equivalent to 11200kg/ha beneath individual tree canopies. By any method this estimate is very high. It does however use a measure of acorn weight (6.3g per acorn) which is high compared to others recorded for this species; and of acorn density equivalent to 215/m^2 beneath trees, a figure obtained from one tree producing a large crop (which he nevertheless felt could be twice as high in an exceptional year). The second highest estimate produced by this method, of 1568kg/ha for *Q. agrifolia*, is also that of Wolf, estimated as an average over a study area of around 64ha. In this case he also estimated yields of acorns of over 7800kg/ha on one area of 46m^2 and in another of unspecified size over 48000kg/ha (at a density of almost 1900 acorns/m^2). All these figures were for an area with an extremely heavy crop. Whether or not these very high estimates are a true reflection of actual yields, or are comparable with other figures, they do illustrate the potential for variability which might be introduced into figures depending on the size of the area from which yields are being calculated; quite apart from whether or not other factors such as tree density or variability of production, are taken into consideration.

7.2.4. Variability in acorn yields

A major feature of acorn yields is their variability (see Appendix 3), between individuals or species, in different places, and at different times. Some of this variability is evident in the figures presented in Tables 12-15. It was impractical to include all the available data illustrating variability in these tables, but more details are available in many of the sources cited below.

Figures illustrating in more detail the potential for variation in weight of individual acorns are presented by Brookes and Wigston (1979). Figures presented by Cypert and Webster (1948) indicate the variation in yields between individuals of one species in one year, as well as the variation in production by these individuals over several years; while data are presented by Tryon and Carvell (1962) indicating the variation between individuals averged over several years. The variation in yields averaged over several years of trees within certain size classes is also illustrated in more detail by figures in Cypert and Webster (1948), Downs (1944, 1949) and Goodrum *et al.* (1971). Goodrum *et al.* (1971), Park (1942), and Trail (1980) present data showing the variation in the numbers of trees of different size classes or species which produced no acorns at all, either indicating differences between several years, or as averages over several years. Data on the differences in production between species at different locations in any one year are given in more detail by Brookes and Wigston (1979), Burns *et al.* (1954), Downs and McQuilkin (1944), Gysel (1957), Havera and Nixon (1980), McQuilkin and Musbach (1977), and Trail (1980).

Data regarding the variation in production of species, or groups of species, between years exists in both quantitative and qualitative form (the latter expressed as, for example, failed, poor, medium, good, and abundant yields), and is given in some detail in several studies, including those of Brookes and Wigston (1979), Burns *et al.* (1954), Christisen (1955), Cypert and Webster (1948), Dalke (1953), Downs and McQuilkin (1944), Goodrum *et al.* (1971), Griffin (1971), Gysel (1956, 1957), Havera and Nixon (1980), Henry and Conley (1972), Kenward and Holm (1989), Korschgen (1962, 1981), Nicholas and White (1984), Nixon *et al.* (1975), Park (1942), Sharp and Sprague (1967), Smith and Scarlett (1987), and Tryon and Carvell (1962).

Much of the data available regarding variation between or within species over time comes from fairly short-term studies, and though several of the studies appear to provide support for either synchroneity or complementarity of production between species or groups, they are only tendencies, and in general it is not possible to say that either suggestion is more likely to be correct than the other. Considering the great complexity, and lack of understanding, of those factors likely to be important in relation to the production of acorns (see Appendix 3), this is perhaps not surprising.

7.2.5. Acorn yields - general conclusions

Based upon the available data, and the discussion here and in Appendix 3, it is possible to come to some generalisations regarding patterns of acorn yields.

Both annual and average yields can vary greatly between individual trees.
Some trees tend to consistently bear good crops when they bear a crop at all, others consistently poor crops.
More trees tend to bear crops in years when there is generally good production.
Average annual yields of individual trees will tend to change through the life cycle of that tree, relating to both size and age, though in some cases these effects may be overridden by other variables.
Average yields of individual trees or species may vary greatly between different sites, either on a regular basis, or in any one year.
Where several species occur together heavy, medium, and poor yields may occur synchronously, or they may not.
In some places they may occur synchronously, in others they may not.
In some years they may occur synchronously, in others they may not.
Where only one species is present heavy, medium, and poor yields of individuals or populations may occur synchronously, or they may not.

Therefore, while in some cases, more or less irrespective of site or region, there may be very heavy, or very poor crops by any one species, or several species, in other cases there might, for example, be widespread heavy crops, or crop failure, in which individual sites, populations or species may show a different trend. In other cases there may be a range of variation between sites, populations and species, but this variation will not be predictable based upon previous production.

In general the data are not sufficient to come to any conclusions other than the most general regarding annual variation in crops, or the likelihood of crops being available in one area at one time. Most studies suggest that some acorns are produced in most years, but some find that there will be large-scale crop failures, even where several species are present in one area. In regions where only a few species are present, the importance of variability between individuals may become more important, so that there may on occasion be complementary effects within a species. One species may fail over a very large area, or it may show variation between sites.

7.3. LOSSES

7.3.1. Introduction

So far this assessment of the data has been concerned only with estimates of the gross yields of acorns produced by oaks. Apart from the immature category, which is unlikely to

contribute towards a usable yield, not all of the gross yield would necessarily be accessible, or available, to people. It might include categories of acorns which would be unusable or less attractive, because of damage by invertebrates or pathogenic organisms; and there might be strong competition for good acorns by avian and mammalian predators (see Appendix 4). Some estimation of the quantities of acorns which may be damaged or destroyed before, during, or after ripening is essential in estimating ueable yields; and is discussed next.

7.3.2. Estimates of losses from the acorn crop

Several studies of acorn production have included estimates of the percentage of total yield damaged or destroyed, or removed by animals. Estimates of the numbers of aborted or underdeveloped acorns have also been made. This data is shown in Table 16. Damage by, or losses to, vertebrates and invertebrates are shown as percentages of fully-developed acorns. As noted in Appendix 3 many flowers and developing acorns are lost during early stages of development. Only those underdeveloped or aborted acorns which persist on the trees until the time of acorn drop or shortly before, and which could potentially be included in estimates of yields made at this time, are included in Table 16. Since these can not generally contribute towards a usable yield they are treated separately in the Table, as a percentage of the total yield of fully-developed acorns.

7.3.3. Estimates of acorn requirements by wildlife

Apart from estimates which have been made of the quantities of acorns removed by animals, one source of potential information on the possible intensity of competition from vertebrate competitors is provided by estimates of the yields of acorns which are thought to be required to support populations of certain species.

In eastern North America Shaw (1972, cited in Verner 1980), based on several studies undertaken in the east and southeast, estimated that 112kg/ha would provide for animals of both game and non-game species. Nixon *et al.* (1975) estimated that a total of 58.9kg/ha sound tree seed (including both acorns and hickories) was necessary to support a good squirrel density in Southeastern Ohio. Goodrum *et al.* (1971) estimated the acorn-yield requirements for quail, turkey, squirrels and deer in pine and pine-hardwood forests of Louisiana and Texas, and suggested figures ranging, for the different species, from 0.4kg/ha to 25.2kg/ha for 180 days feeding, or 0.7kg/ha to 42.0kg/ha for 300 days feeding; with totals for all species combined amounting to 57.0kg/ha for 180 days or 95.1kg/ha for 300 days. These figures exclude requirements for other non-game species present. For the same requirements and animal densities for quail and squirrel, but with

deer at 20 times the density suggested by Goodrum *et al.*, Potter and Johnston (1980) suggested that in California 275kg/ha of acorns would be required. They also suggested that losses to other causes (including both insect damage and failure of acorns to develop) would account for 50% of the crop, and therefore doubled the figure to 549kg/ha.

In one European study Turcek (1967, cited in Corbet 1974), estimated a total of 54.6kg/ha lost to wood mice (45kg) and bank voles (9.6kg), feeding for 180 and 120 days respectively. In Britain Shaw (1968, cited in Evans 1988) estimated that total predation of acorns could amount to 200kg/ha.

Others have provided estimates of consumption or requirements per day. Bowyer and Bleich (1980) noted that in one year with an extremely heavy crop Californian deer were consuming 1.2kg dry weight each of acorns per day, and a similar figure of 1.1kg each per day is suggested by Potter and Johnson (1980). For a 90-day period these figures are equivalent to 108kg dry weight, and 99kg. Tanton (1965, cited in Corbet 1974) estimated that a population of 60 rodents per hectare would eat 0.16-0.32kg dry weight/ha/day. Over 150 days this would total 24kg and 48kg dry weight/ha. Jones (1959) estimated that removal of acorns from the trees by wood pigeons totalled 400g/day each, equivalent to 36kg per pigeon over 90 days.

Such figures are useful in that they can be directly compared with actual estimates made of yields, and give some idea both of the yields of the trees in the areas in which the studies were made, and of the potential losses. However, there are few such studies, and they do not include all possible losses from the potential yield. It is not always possible to compare these figures with the total yield at the time and place at which they were estimated; and perhaps more useful are the estimates which have been made of the percentages of crops potentially lost to various sources of damage.

7.3.4. Problems with estimates of losses

An examination of Table 16 indicates that there is considerable variation in estimates of damage to, or losses from, the crop yield. Some of this variability may be due to problems of comparability between studies such as discussed in relation to estimates of yields (see 7.2 above), but further factors may also be involved.

7.3.4.1. Pre-ripening losses

As noted in 7.2.2.1., removals of acorns from the trees by birds and mammals mean that many counts underestimate the total potential yield. Most estimates do not differentiate the

time and place of removal or damage, but merely record estimates of percentages of the crop lost to vertebrates. Depending on the types of observations made these figures may or may not include all possible categories: acorns removed from trees (where cupules were not removed, and later fell to be counted); acorns damaged or eaten in trees (from empty shells or cotyledon fragments); and acorns eaten, damaged, or removed from beneath trees.

Only a few studies have attempted to quantify the first two categories of losses. Estimates of removal of acorns from trees by arboreal feeders include 13-14% (Cypert and Webster 1948), 14% (Christisen and Korschgen 1955, cited in Goodrum *et al.* 1971) and 18% (Tryon and Carvell 1962). Cypert and Webster (1948) also noted a further 5-14% of the crop eaten in the trees (indicated by empty shells beneath trees), and from 12%-37% acorns damaged in the trees (estimated from partly-eaten pieces). Wood (1938) recorded from 9-50% of acorns taken from the trees by grey squirrels. Downs and McQuilkin (1944) estimated damage to acorns on the trees by birds and squirrels averaging from 12%-48% for five species over seven years. This study, like many others, excludes any estimate of acorns completely removed from the trees.

In terms of quantifying total production such figures suggest the range of possible underestimation of figures of yields calculated from counts of acorns collected in traps. They also suggest the kinds of adjustments which might need to be made to figures of loss estimates which only measure losses on the ground, as do most of those included in Table 16.

7.3.4.2. Time of measurement of acorn losses

A particularly important factor which can affect estimates of losses is the period of time within the season over which a survey is undertaken. Where information regarding this is available it has been included in Table 16. Some estimates include only losses of acorns during the time of acorn fall, others extend into the following spring, or even longer.

This factor is particularly complex, since, as Appendix 4 suggests, the rate at which fallen acorns are removed by animals can vary greatly between places and years, relating to such factors as the size of the crop, availability of other foods, the numbers of animals present, and perhaps the particular oak species involved. Estimates of losses to insects may also be affected by this factor. Large numbers of acorns which appear sound at drop may actually be infested (see Appendix 3, 3.2.7.; Downs and McQuilkin 1944; Hilliard 1986; Korstian 1927), and this may only become apparent in estimates made later in the season.

7.3.5. Acorn losses - general conclusions

The following conclusions are based on the discussion above and those factors affecting losses discussed in Appendix 4.

There is little good quantitative evidence for preferences for particular species of acorns, and acorns of different species seem to be used mostly in relation to their relative abundance.

In North America the total losses of acorns of the high-tannin red oaks may be as high as those of the supposedly more palatable and preferred white oaks, though, all other things being equal, red oak acorns tend to remain available for longer after falling than do white oak acorns.

There may be considerable differences in estimates of losses of acorns both between and within studies.

There may also be considerable differences in losses from year to year.

When and where yields are low acorns may all disappear very rapidly.

When and where yields are high acorns of all species may remain on the ground throughout winter and well into the following year, sometimes as late as the next year's drop.

There is therefore considerable potential variation in the likely available yield of acorns. Even very local differences may occur due to variations in such factors as crop size, both in the immediate locality and throughout the adjoining region, the animal species present, the density of their populations (which may relate to previous acorn crops as well as to other ecological relations), the abundance of other food in the environment (especially of other mast crops), and perhaps the particular species of oaks present. The period of availability will also vary considerably due to a combination of these factors and others affecting ripening and timing of fall of acorns.

7.4. NUTRITIONAL DATA

Models of past subsistence which attempt to use quantitative measures (such as optimisation models) often require the production of estimates of the available nutritional input from the resources considered - yield purely in terms of raw material is not sufficient. For this, as well as estimates of available yields, quantities of nutrients present in acorns or their energetic values need to be estimated.

Much of the available data on nutritional components of acorns derives from studies by wildlife biologists. However, nutritional analyses have also been undertaken by others

interested in the potential of acorns as a food resource, for livestock or sometimes for humans. Much of this data has been discussed in Chapter 6, shown in Table 8, and summarised in Tables 9-11. In this section some of the problems with this kind of data are discussed.

7.4.1. Problems of comparability of nutritional data

In comparing all nutritional data it must be borne in mind that methods of analysis have varied over time, and that some methods, especially the older ones, have various drawbacks (see, for example, discussions in Atwood 1948; Paul and Southgate 1978; Wainio and Forbes 1941; Watt and Merrill 1963).

Different problems are involved in analyses of different components. There may be difficulties in measuring proteins and tannins when they are present together, as they are in acorns, because of their propensity for combining to produce insoluble compounds (see Appendix 2). Harborne (1984) noted that it is probably only since the mid 1970s that methods of analysis of tannins have become reasonably accurate. Analysis of lipid content may vary considerably according to the methods used (Paul and Southgate 1978). In particular, the commonly-used Soxhlet method can give high readings under some circumstances (Dr. Anthony Leeds, pers. comm.). Measurements of fat in acorns collected by the present author were undertaken by Dr. Anthony Leeds, of the Department of Nutrition and Dietetics, King's College London, using extraction by petrol ether in a Soxhlet apparatus, and repeated using chloroform methanol extraction. Values given by the first method ranged from 11.0 to 21.8% of dry weight, averaging 19.3%, while for the second they ranged from to 1.6 to 8.4%, averaging 7.3%. The use of the Soxhlet method may partially explain the extremely high figures given for lipid quantities by Gul and Khan (1982) and Tripathi and Khan (1990) (see Table 8). Measurement of carbohydrate is particularly difficult to interpret. In many cases it is calculated by difference, as the proportion of 100% remaining when other constituents have been quantified, though this is considered to be an inaccurate method of estimation (Paul and Southgate 1978). There may be problems with direct measurement too, as suggested by work undertaken by Koenig (1991), whose analyses of structural and non-structural carbohydrates in some Californian acorns produced results with large discrepancies.

7.4.2. Moisture content, and the basis for expression of figures

The figures shown in Tables 7-11 are expressed as % of dry weight, except those for moisture, which are as % of total acorn weight prior to analysis. In some cases it was necessary to convert figures given on a fresh weight basis to a dry weight basis. In other

cases it was not possible to do this, and some figures in Table 8, notably those provided by Bonner (1971, 1974), Koenig and Mumme (1987) and Koenig and Heck (1988), are very different from others, possibly because they are expressed on a fresh weight basis, though this is not clear from the sources.

Moisture values in the tables are as given in sources, and vary considerably. As the figures for moisture values indicate, not all acorns were in a similar state of freshness when analysed, though it is uncertain how this would affect their nutritional value (it could certainly affect such biochemical processes as after-ripening - see Chapter 6). Tannin values are also expressed separately, as a percentage of dry weight where possible; though in some cases it was not clear from the source on what basis these figures were expressed.

7.4.3. Energy values

Very few direct analyses of energy values of acorns by bomb calorimetry have been undertaken. Those that have are included in Table 8, expressed as kJ/g of dry weight, though again there are some instances where it is not clear from the source whether estimates are expressed on a dry or fresh basis. Energy values were also calculated from the values of the proximate constituents (see Appendix 1, Notes to Nutrition Tables) for all samples where possible. These calculations must be treated with particular caution, since they are directly dependent upon the data provided in the analyses, which, as suggested above may not always be strictly comparable.

Table 11 shows the averaged data on energy values for acorns from different regions and taxonomic groups. As in Tables 9 and 10, discussed in Chapter 6, processed samples were excluded, and, for the calculated values, those where the components from which calculations would be made were not from a total approximating 100%. Becase the data on which any calculations for the Eastern Asian region would be made are not of comparable quality (see 6.2.), and few analyses are given directly in sources, no attempt was made to present averaged data for this region.

Average values for the *Erythrobalanus* group are consistently higher than for the *Lepidobalanus* group both in the east and west of North America, but the ranges of values for individual species show considerable overlap. Despite the greater quantity of high-energy lipids present in North American acorns, the average energy values do not differ greatly between here and Europe, as they would be expected to, in relation to the differences between *Erythrobalanus* and *Lepidobalanus.*

7.4.4. Shells and fibre content

Most figures in Table 8 are for acorns without shells. In some studies where this is not the case this has been indicated, but not all sources specified which components of the acorn were analysed. As discussed in Chapter 5, there are inter- and intra-specific differences in shell thickness as well as the percentage contribution of shell to the total acorn, and Table 8 shows figures for fibre content of samples which included shells ranging from around10% to over 25%. Petrucci's (1947) study of acorns in Italy included analyses both with and without the shell. Differences were greater in acorns analysed without shells, apparently because acorn kernels high in nutritive value were compensated by shells low in components. Gaussen and Rouquette (1949) noted that some of their figures for fibre values for acorns were biased by the inclusion of pieces of shell which they were not able to separate before analysis.

It cannot be assumed that all analyses showing high fibre values include shells. Braude (1943) reports separate analyses undertaken on whole acorns, cotyledons, and shells. While whole acorns contained 21% fibre, shelled cotyledons contained almost 17% (shells alone contained 36%; which compares with other figures for shells alone of 55% (King and McClure 1944) and from 35 to 58% (Petrucci 1947). Although Braude's fibre value for cotyledons alone seems high in comparison with others (e.g., 2.5% (King and McClure 1944), 2.4 to 4.5% (Petrucci 1947), and others all of a similar order) Billingsley and Arner (1970) also analysed acorns of *Q. nigra* without their shells, and found 14.5% fibre. These were mature acorns, though not well-developed due to a poor growing season.

Whether or not the fibre content in any analysis is quantified separately will particularly affect estimates of carbohydrate content. The fact that many of the analyses included in the European region did not distinguish fibre, while many North American ones did, possibly explains the relatively high average carbohydrate value for the former group shown in Table 9 (see 6.2.3.), as well as the high energy values of European acorns in comparison with American white oaks noted above.

In a comparison of energy values of acorns analysed with and without shells (shown in Table 11) the average values for both the eastern North American samples, and those from Europe show consistent differences, with samples with shells averaging 1kJ/g lower, and those without 1kJ/g higher than the totalled averages. There is a large overlap in ranges of values. No such differences are apparent in the western North American data. In addition to the relatively small number of samples from this region, many of the fibre values are high, and it is possible that more samples than those indicated as such in Table 8 included shells.

7.4.5. Other problems

Apart from problems relating to the methods of analysis there are other factors that should be borne in mind when comparing figures from different studies such as those presented in Tables 8-11. These include the likelihood of variability in nutritional qualities discussed in 6.4, due to inherited or environmental differences. In particular, the precise origin of acorns contained within samples, whether all from one tree, or a combination of acorns from many individuals, may have an affect on the analyses, but such details are not often specified in sources. Such factors as the condition of acorns when collected and the length of storage period prior to analysis may also be imortant (see 6.4.1.).

7.4.6. Summary of nutritional data

Some general conclusions about the nutritional and biochemical properties of acorns can be made.

The most significant differences between acorns of different species are in the quantities of fats.

The exclusively North American red oaks are markedly higher in this constituent than other taxonomic groups.

Some individual species within other groups have relatively high fat content but this does not generally appear to approach the values recorded for red oaks.

The proportions of carbohydrate tend to be smaller in the red oak group.

There are relatively small differences in proteins between species, and differences do not seem to relate to taxonomic groups.

In North America red oaks tend to be higher in their energy value than are white oaks.

Energy values for individual species overlap considerably.

Since there are relatively few direct analyses of energy value, and other estimates depend upon accurate quantification of fats, proteins and carbohydrates, energy values should be treated with particular caution.

Acorns of some species are more astringent than others.

Although the red oak group is generally said to have more astringent acorns than members of the white oak group, the quantitative data on tannins suggests considerable overlap. The available quantitative data from other parts of the world is insufficient to come to any other conclusions, though Japanese members of sub-genus *Cyclobalanopsis* seem to be particularly

low in tannins. There may be variations in the proportions of sugars present in acorns which affect their taste.

There may be considerable differences in nutritional and biochemical constituents between analyses of acorns of the same species. There is insufficient data to conclude whether the most important differences are due to genotype, environmental factors, differences in methods of analysis, or other factors. There may be significant differences in constituents of acorns depending on time of harvest, or period of storage, relating to the metabolic condition of the acorn (depending upon, for example, factors relating to ripeness, dormancy or germination).

Because of the problems discussed above, together with the lack of understanding of many of the factors producing variation in nutritional composition, and because of the paucity of nutritional data on many species and in many areas, it must be emphasised that the published nutritional data can only be used in the most general way. The tables of averages in particular should be treated with caution.

7.5. CALCULATING AVAILABLE NUTRITIONAL YIELD

Data on yields, losses and nutritional values all need to be considered when attempting to make quantitative estimates of the available nutritional yield from acorns. The discussions above have indicated that there are potentially considerable problems in attempting to do this accurately.

When modelling the potential past use of acorns there are other important considerations to be included, including the problems of extrapolating any modern quantitative estimates into the past, and the need to consider the effects of human behaviour and decisions. These, together with the ways in which the kinds of data discussed in this chapter have been used, or sometimes misused, by those attempting to model the past use of acorns are discussed in the next chapter.

CHAPTER 8. MODELLING THE ROLE OF ACORNS IN HUMAN SUBSISTENCE - PROBLEMS AND POTENTIAL

Having examined the ethnographic data on the use of acorns, and the nature of the available information on those biological characteristics which might affect their use by people, it is possible to examine the archaeological interpretations that have been made about acorn use in a more critical light.

8.1. THE ROLE OF MODELLING IN STUDIES OF ACORNS AS A HUMAN FOOD RESOURCE

8.1.1. The use of biological and ecological data in modelling the role of acorns

8.1.1.1. Estimating yields of acorns

As indicated in Chapter 2, many attempts at interpreting archaeological finds of acorns have drawn on biological information, both quantitative and qualitative, about acorns, and such information has often formed the basis of "models" of past acorn use. Data on yields (including mast cycles, factors affecting productivity, losses to animals and insects, etc) and nutritional qualities (usually in terms of proximate nutrients or calories) are regularly cited, often with reference to a rather limited range of the better known studies, in some cases from other regions, or even continents. It is sometimes unclear why such data are included in archaeological studies, other than to give a general impression of the potential local yield and nutritional value of the resource. In addition, unless it is related to data on other areas, or other resources, such information may be relatively meaningless.

Other studies have incorporated data into often quite complex quantitative models, relating the values to those of other resources. Tryon and Carvell (1962) have noted that, although estimates of yield in acorns can not be expected to be accurate, any discrepancies in measurements should be proportional if the same methodology is used, so that estimates are acceptable as comparative values. Quantitative models of resource use apparently follow this same line of reasoning and require not necessarily accurate, but at least comparable, estimates of modern productivity. Whether this is actually achieved is open to question. The problems with making and using quantitative estimates of yields and nutritional values of acorns, and the uncertainty surrounding the causes and correlations of many of those characteristics relevant to such resource modelling, have been discussed at some length in Chapter 7. In theory, measurements carried out over a number of years should enable

estimates of average modern production from areas with given densities of trees of given species, or combinations of species, to be made. There are however relatively few such long-term studies, and many models necessarily therefore draw on somewhat insubstantial data, or data which may not be relevant to the area under discussion. Variability is perhaps the most important factor when considering yields of acorns (see Appendix 3), yet it is rarely taken account of in models of past food potential. Figures used in the quantitative models discussed in Chapter 2 are usually for average production. However, for acorns and other crops with similar large periodic variations, averages may not be the most useful measure of production. It may be that the frequency, or size, of small or large crops is more important in relation to utilisation.

For many models, especially the more complex quantified models, difficulties with the available data are compounded by the large number of assumptions and pieces of guesswork which are required. The ease with which it is possible to introduce errors because of incomplete understanding of the available data can be shown by reference to some of the attempts made to model acorn resources.

As discussed in Chapter 7, the problems of using figures on certain aspects of yields and multiplying them up may introduce discrepancies into figures. In particular the general problems of converting figures in bushels to kilograms have been discussed in 7.2.2.2, and various conversion factors have been used in resource models (see, e.g., Baumhoff 1963; Mayer 1976; Schulz 1981). Keller (1987) calculated the yields of oaks and other nut trees found in part of the Lower Mississippi Valley, and having allowed a conservative estimate of availability to people of only 10% of the estimated crop, calculated that enough calories would be available from nuts, if these constituted 100% of the diet, to suport a population of 324 people per square mile, or at 25% of the diet 1298.4 people per square mile. He suggested that this great subsistence potential brought into question any need to develop agriculture, and that it may have been "more a consequence of cultural and technological considerations than of natural factors". Unfortunately Keller's arguments are undermined by a closer examination of the figures. Mean production per tree of 0.875 bushels for all oak species except *Q. macrocarpa* (1.125 bushels/tree) were multiplied by the average cleaned seed yields per bushel of fruit derived from the handbook of "Seeds of Woody Plants in the United States" (USDA 1974) to give average yields per tree ranging from c. 16kg to c. 56kg. In comparison with measured total acorn yields per tree (which should be higher than figures for cleaned seed) from two sources also cited in the same paper average figures ranging from 1.4 to 3.8kg/tree are available (see Downs 1944; Goodrum *et al.* 1971 - Table 13). It is uncertain where Keller derived his figures on estimates for mean production/tree from, though they are within the range of figures apparently derived from the first edition of the USDA handbook, of a range of 0.25 to 1.5

bushels/tree, which have been used in other North American acorn models (e.g., King 1976a; Zawacki and Hausfater 1969). When the average yields in bushels are converted to kg/tree using the figures given for weight of a bushel of fruits given in the USDA handbook, they range from a minimum of 3.5kg to a maximum of 88.5kg. Values for *Q. alba* range from 10.5 to 62.9kg/tree and for *Q. rubra* from 20.6 to 41.3 kg/tree. These figures seem very high compared with yields obtained from specific studies such as those listed in Table 13. The use of the USDA data in resource models, and it's likely overestimation of actual yields, has also been criticised by Petruso and Wickens (1984). In California a similar situation apparently exists, where the data on acorn yields of Wolf (1945) has been heavily drawn on (see, e.g., Baumhoff 1981; Gould 1975; Mayer 1976 and Schulz 1981). As indicated in 7.2.3., Wolf's data are at the high end of the estimates of yields that have been made (see also Basgall 1987).

There are other problems with estimates of yields encountered in the archaeological literature. King (1976a) estimated the potential yield of eight species of *Quercus* and several other nut trees in the vicinity of the Rodger's Shelter site in Missouri, again using generalised data derived from the USDA publications (see above). King commented that an additional factor to be accounted for was the fact that acorns of the red oak group take two years to mature, and that therefore only half the trees would produce a crop in any year, which is not the case. Red oaks in any one year bear both the maturing crop originating in the previous year, and acorns of the current year which will mature the following year. The yield figures for these species were adjusted by King, halving the values of all red oak yields. Though the figures were not used in any subsequent form of modelling, or related to the archaeological data, and irrespective of the problems already discussed with the data used in the estimates, they were nevertheless substantially underestimated.

Mayer (1976) also contrasted the one-year and two-year species in California and noted that two of each group were most commonly used by the Sierra Miwok Indians, suggesting that they adjusted their use depending on the annual abundance of the two groups. Mayer seems to be making a fairly common assumption encountered in the biological as well as archaeological literature, regarding the "natural backup system" of the one- and two-year maturation periods of the two oak groups (see also Keller 1987; Lopinot 1982) which an examination of the data on yields and cyclicity has demonstrated is not consistently the case (see 7.2.5.; Appendix 3).

8.1.1.2. Relating data on yields and availability to the past

The problem of extrapolating information derived from modern studies into the past is probably the most widely acknowledged difficulty with the use of such data, as well as one

of the least surmountable (see 2.2.2.3.2.). However, some significant problems have not apparently been considered in modelling.

Firstly, the modern environment may have been considerably modified by human activity, affecting such things as absolute numbers and distribution of trees, age structure of the tree population, and numbers of predators or competitors for acorns. Modern imbalances in animal population densities have been noted by foresters and wildlife biologists who have attempted to estimate use of acorns by vertebrates. Imbalances may relate to both increased numbers of small mammals due to recent human destruction of carnivores (Watt 1919; Wood 1938), and to the introduction of domesticates (Bowyer and Bleich 1980; Griffin 1980a). Introduction of wild species outside their range, or of the favouring of certain species for game hunting might result in similar effects. Many of these, and similar studies, have attributed the poor seed reproduction which appears to have been affecting oaks in many areas, to such imbalances, resulting in excessive predation on acorns, though others have argued against such an explanation (Mellanby 1968). In Britain, where North American grey squirrels have been introduced, it has been noted that, despite often favouring acorns as food, they have little impact on the crop, unless it is very small (Corbet 1974). The inability as yet to discover satisfactory explanations for the failure of oaks to regenerate suggests that much has yet to be discovered about the subject. Nicholas and White (1984) discussed the inter-relations between animal population densities of native wildlife and introduced domesticates, and mast yields of acorns, but noted that few models had been properly developed or tested. The potentially significant effect that such differences in modern animal populations could have on estimates of acorn availability to people based on modern data does not seem to have been examined in attempts by archaeologists to extrapolate quantitative data on animal uses of acorns into past situations.

Secondly, the past environment may have been modified by human activity, in a different way to modern modification. Many studies have emphasised the need to use "natural" or "virgin" forest as the closest analogy with vegetation as it would have been when utilised by "archaeological" populations. There is considerable ethnographic data on the burning and opening up of forests, by hunter-gatherers and other "traditional" people, which, together with information on the likely responses of oaks to such activities, and the recognition that oaks may often owe their position in modern ecosystems to disturbance of some kind, has been discussed in 4.6. If such activities were undertaken in the more distant past it is likely that "virgin" forest may not in fact be a good analogy with that in the vicinity of past archaeological sites.

Though the potential effects of human activities have been acknowledged by some archaeologists (see 2.2.2.3.2.; also Lopinot 1984; Reidhead 1984), the effects on acorn, or

other nut tree, yields have not been examined in resource models. Most of the models discussed in Chapter 2 are static, and attempt to relate a hypothesised "environment", as an independent variable, to the archaeological record, or sometimes to changes in the archaeological record. However, acceptance of the possibility that the environment is not static, and that some of its most important variations may be due to human activities, suggest an alternative role for modelling than that of attempting to recreate past resource abundance. There are many potential areas of investigation in relation to the effects of human activity on acorns. In particular, opening up of forests, whether by burning, cutting of trees, or browsing by animals may have the effect of increasing acorn yields of individual oak trees considerably, because of factors such as increased light, and opportunity for canopy growth (see Appendix 3, 3.3.1.3.3.). The point at which such activities would constitute over-destruction of oaks has been an area of debate, especially in regions such as the Mediterranean, where the effects of human activity have generally been considered to have resulted in "degradation" of the environment, and destruction, or change in the balance of species, of oaks (see 4.6.; also Lewthwaite 1982; Rackham 1982). It can be argued that investigations of the relative effects of potential human activities on resources such as acorns would be a more useful role for modelling than an attempt to relate a fixed model, dependent on many assumptions and much guesswork, to an inevitably uneven and biased archaeological record. As has been pointed out in 4.6. the extent to which past "disturbances" of the environment can be related to human activity is complicated by incomplete and changing understanding of natural disturbance responses. Nevertheless, if archaeologists wish to include discussion of such effects, as they appear to do, study of such responses must be seen as much an area of research within archaeology as it is within ecology and biology.

8.1.1.3. The role of animals

As has been indicated by the preceding discussion, the role of animals in relation to acorns in the past could be an important area for investigation. However, animals do not only constitute competition for the acorn resource from the human point of view. Acorns can be used indirectly by people when animals which feed on them are killed and consumed. Because oak trees are a focus of attention for many species, particularly around the time of ripening of acorns, deliberate targeting of such areas would be an effective hunting strategy, as was indicated by the ethnographic data in 3.2.1.3. and 3.2.2.2.1. The past interactions between people, acorns and animals have been examined in some studies, principally with relation to North American deer (Gage 1979; Purdue 1986; Smith 1974). In Eurasia the presence of domestic animals introduces another factor which should be considered in modelling the use of acorns by people. The area of distribution of putative ancestors of the four early ungulate domesticates of the Old World - sheep, goat, cattle and

pig - encompasses practically all of the area in which temperate Old World oaks occur, with wild pig found through much of the geographical area of distribution of oak species within the Tropics (Davis 1987).

Though pigs are generally viewed as being associated with wooded environments, sheep, goat, and to a lesser extent cattle are thought of as animals of more open habitat (see, e.g., Greenfield 1984; Grigson 1982; Hole 1989; Legge 1989). Their presence is often viewed as inimical to woodland vegetation, and grazing and browsing, by these animals as well as clearance of land to create pasture for them, are viewed as some of the principal factors causing forest destruction throughout Eurasia. Such a view is implicit in some of the models of the transition to agriculture in Southwest Asia which have explicitly considered the role of oaks (Bainbridge 1985b; Bohrer 1972). Both these authors have suggested a role for acorns as a pre-agricultural human food source in the region, but have suggested that the presence of goats, browsing or being fed on oak forage, resulted in destruction of the oak forests and an increasing focus on members of the Gramineae as human food.

However, little is known of the ecological relationships of the wild precursors or early forms of the domesticated species, or of early forms of the domesticates. Analogies for past relationships between these species and woodland are therefore largely drawn from knowledge of modern or historical ecology, behaviour, and management practices. Garrard (1984) used information of this type, together with information derived from the fossil animal communities with which remains of these species have been associated, and summarised what are postulated to have been the habitat and feeding behaviour of the precursors of the Southwest Asian domesticates. Wild cattle and pig were primarily considered creatures of wooded environments (forest or open woodland), with wild sheep preferring steppe, and wild goat favouring a craggy landscape. All species both graze and browse, with sheep apparently having a preference for grazing. However, Garrard emphasises that changes in the environment, due either to climatic factors, or to human impact on both animal populations and vegetation introduce uncertainties into data on habitat preference and food selection. The extent to which a truly open environment is essential for these animals is not certain, and Clason (1984), discussing the introduction of domesticated animals into the Netherlands, suggested that early forms may have been adapted to the more or less closed deciduous forest present, and that the clearance of landscape may have resulted in selection for forms adapted to more open habitats. Factors such as animal population densities, as well as management practices, will interact in determining the amount of open habitat required or produced intentionally or unintentionally.

The extent to which the presence of domesticates necessarily leads to the destruction of oak trees is an area which requires investigation. As noted above, though domesticated species have been implicated in modern studies on the failure of oaks to reproduce, the combination of many factors seems likely to be important. Similarly, the extent to which there has been destruction of woodland in the Mediterranean region, and similarly in Southwest Asia, and to which this is due to human activity or climatic change, is an area of continuing debate (see 4.6.1.3., also Blumler 1991, Huntley 1988; Naveh and Dan 1973; Pons and Quézel 1985; Rackham 1982). The ability of oaks to regenerate vegetatively has been emphasised (4.3.4.5.; 4.6.) and oaks can be maintained, either with or without human intervention, in areas where browsing occurs (4.6.2.). In addition there are examples of the use, and sometimes the deliberate management, of oaks as sources of browse for domesticates from various parts of Eurasia (Burkill 1935; Gul and Khan 1982; Rackham 1976), including southeastern Turkey (personal observation).

Much agricultural literature has viewed acorns as poor, or even dangerous, food for livestock, largely because of the presence of tannins (see Appendix 2, 2.4.). However, these toxic effects seem to occur generally in extreme circumstances when sufficient feed of other kinds is not available, and feeding studies with domesticated animals have demonstrated that, as long as sufficient protein is available, acorns, even in large quantities and fed to modern breeds, are not harmful, and can be a valuable foodstuff (Braude 1943; Downs 1949; Duncan and Clawson 1980; Ministry of Agriculture and Fisheries 1940; Wagnon 1946, cited in Duncan and Clawson 1980). Acorns are an important food for cattle and goats in Israel (D. Zohary pers. comm.). Cattle introduced into North America may feed heavily on acorns (Duncan and Clawson 1980; Wolf 1945), as do goats (Smith 1929); and acorns are collected for feeding to goats in Turkey (personal observation), and possibly horses in Israel (D. Zohary pers. comm.).

Domesticated animals do not necessarily therefore, have to be viewed as inimical to oaks, and acorns do not have to be viewed as inimical to domesticates. Acorns could potentially constitute either human or animal food, or both, in a system incorporating domesticated animals. Whether acorns were abundant enough to provide both people and wild or domesticated animals with food; and to what extent people would consume acorns directly or "prefer" to utilise them indirectly is another area which has been little examined in resource models, and constitutes another important area for future investigation.

8.1.1.4. Summary

The criticisms that have been made in the preceding discussion of the use of various types of biological data in modelling are not meant to imply that such information should not be

used, nor that attempts to quantify resources in terms of their yields are necessarily doomed to failure. Explicit quantification is at least amenable to explicit criticism. However, studies that draw upon such information need to show some appreciation of the problems of using data of this kind. The emphasis on testing the archaeological expectations of models has meant that the assumptions relating to the resources themselves have often not been examined in great detail. If archaeology is to use such information however, it can be argued that these data are as important as the archaeological data which they are being used to interpret. Starna and Relethford (1985) commented on the less than adequate use of biological and ecological data and concepts in archaeological literature, and Rhoades (1978, 612) discussed the "archaeological use and abuse of ecological concepts". This study was particularly concerned with the use by archaeologists of the concept of the "edge effect" on increasing the density of animal populations at ecotonal boundaries, despite the absence of evidence for this in ecological studies. Rhoades concluded that "we need to take a closer, critical look at the ecological terms and wildlife studies to which we give so much credence. Without questioning the analytical constructs and empirical findings of sister disciplines, we run the risk of basing research strategies on 'false principles' and .... falling victim to a self-fulfilling prophecy of our own making".

8.1.2. Incorporating human behaviour and activities in models

8.1.2.1. Estimating the costs of acorn use

Some modelling of acorn use has involved consideration of the effects of some human activities, specifically those to do with use of the resource itself. Simms (1987), for example, has argued that productivity may bear little relation to human use of a resource, and that the costs and benefits of procurement of resources are more relevant. Several models have attempted to incorporate estimates of such costs, and have been based on experimental collecting and processing of resources, together with ethnographic data on both the methods and times involved in such activities. One of the first studies to deal with acorns in such a way was that of Reidhead (1976), who estimated yields, collecting and processing costs of various plant and animal resources in the vicinity of the Leonard Haag site in Indiana. Total estimates of costs for one white oak species (*Q. alba*), and two red oak species (*Q. rubra* and *Q. velutina*) were based on collection rates, transport and storage costs, shelling costs, and leaching costs. Reidhead suggested that because white oak acorns were smaller than those of the two red oaks they would take longer to shell. He cites studies later published by Petruso and Wickens (1984), who, in actual processing experiments, found shelling of *Q. rubra* and *Q. velutina* more time-consuming than that of *Q. alba*. He also suggested that white oak acorns do not need to be leached, which both the ethnographic data and Petruso and Wickens' study suggest not to be the case. Strangely,

while Reidhead described the common boiling method used for leaching acorns in eastern North America he did not attempt to estimate costs of this, but of what he suggested was a more cost effective method of roughly smashing acorns, and placing them in baskets in running water. Reidhead's intention was to produce estimates of costs relative to other resources, for use in an optimal foraging model, but it is difficult to assess the applicability of the model, because many of the costs were estimated arbitrarily, including the costs of transport and storage, the costs of shelling white oak acorns, and the costs of leaching. Estimates for other resources included similar arbitrary estimates.

Other studies which have estimated the costs of various aspects of human uses of acorns have in some instances shown a wide divergence from the estimates made by Reidhead. Collection rates ranging from 25kg/day to 34kg/hr have been made in California (Basgall 1987; Mayer 1976; Smith 1929; Wolf 1945). Simms (1987) in the Great Basin estimated rates of 1.7kg/hr collected from the ground, and 0.4kg/hr picked from trees. In the east Reidhead (1976) estimated a collection rate of 15kg/hr, and Petruso and Wickens (1984) an average for four species of 12kg/hr. Rowley-Conwy (1984a) cites Perlman's (1980) collection rates of North American species, of 12-24kg/hr, though Perlman's own estimates (1980, 280, Table 6.2) show a range of from 0.2-1.6kg/hr for "small nuts" (apparently just small acorns - *op. cit.* Fig. 6.8) or 1.8-6.4kg/hr for "large nuts" (large acorns and pecans). Rowley-Conwy's own collection rates, undertaken in Europe, were calculated from numbers of acorns collected, and were expressed in terms of return rates in kcal/hr, using Baumhoff's (1963) estimate of 5000kcal/kg (20.9kJ/g). When converted, using Rowley-Conwy's estimate of 4g/acorn, the return rates are equivalent to 4.5-7.0kg/hr. Baumhoff's data however included acorns of the Californian red-oak group, with high fat content and caloric value, and the return rate is likely to be an over-estimate for the *Q. robur* acorns to which Rowley-Conwy is extrapolating (see Table 8). Rates estimated for pounding acorns include 1.4 kg/hr from Californian ethnographic data (Basgall 1987; Waugh 1987), while Reidhead pounded coarse flour at the rate of 4kg/hr. Basgall gave a leaching time of 0.7kg/hr for the California sand-basin method, while Reidhead "guesstimated" 6.7kg/hr for leaching in baskets in a stream. Unfortunately none of these studies has examined the relative costs of collecting acorns in different areas or of processing acorns in different ways, and rarely have they examined differences between oak species, so that it is difficult to know to what extent the figures can be compared with each other, and to what extent differences reflect assumptions made, or differences in methodology.

8.1.2.2. Human preferences and selection of acorns

Reidhead's model, and other discussions of acorn use in eastern North America in particular, have often focussed on the question of preference for acorns of the white or red oak groups. Early studies in particular, and some more recent examples, tended to assume that the less astringent acorns of the white oaks would be preferred by people, largely because of assumed lower processing costs (see, e.g., Munson *et al.* 1971; Egan 1988). However, apparently in parallel with wildlife studies (see Appendix 4, 4.4.6.7.), the suggestion has been made more recently that red-oak acorns might be preferred because of their higher fat content and energy value. Reidhead's study was influential in introducing this view to North American archaeology. However, as the discussion above indicates, the factual basis for better nutritional returns from red-oak acorns is uncertain because of some of Reidhead's assumptions, though the work of Petruso and Wickens (1984) suggests that this may be the case in their study area. Reidhead attempted to find support for preference in the ethnographic literature, and cited Zeisberger's (1885) comment regarding use by Chippewa of "the worst kind of acorn" (see 3.2.2.1.). It is certainly not clear whether this indicates a preference for acorns of the red-oak group, and, as discussed in Chapter 3, the ethnographic evidence in general does not enable any such preferences to be determined. Reidhead's characterisation of red-oak acorns as preferred resources by humans is based partially on their apparent nutritional superiority, together with suggestions of their lower attractiveness to vertebrate and invertebrate competitors, and their persistence ungerminated overwinter, resulting in longer periods of availability, together with better storability.

Others have subsequently repeated similar statements suggesting human selection for red-oak acorns, because of factors such as lower animal competition, including Hilliard (1980), Keller (1987) and Petruso and Wickens (1984). As discussed in 7.3.5. and Appendix 4, the data on animal preferences and insect predation suggest a more complex position than is usually allowed for in the archaeological literature. Reidhead's and subsequent studies have also suggested that acorns, particularly of the white oaks, may be difficult to store because of germination in storage. However, though both Hilliard (1980) and Keller (1987) have suggested that acorns, especially of the white oaks, would need to be parched or processed immediately to prevent germination, both cite data derived from forester's studies of storage of acorns, which relates to storage of live acorns as tree seed. As recalcitrant seeds (see 5.3.4.), a relatively small amount of water loss is sufficient to kill the acorn and prevent subsequent germination. There is almost certainly no need for parching or roasting to prevent acorns germinating in storage, if they have been dried. In fact, since acorns of red oaks are apparently able to lose more water before being damaged in this way (see 5.3.4.), the need for thorough drying would in theory be more necessary for these than for white-oak acorns, if they were to be prevented from germinating in the spring.

8.1.2.3. Potential consequences relating to harvesting, storing and processing of acorns

One area which has been little examined in modelling acorn resources is the effects of variations in methods of harvesting, storing, processing and cooking of acorns.

8.1.2.3.1. Harvesting

The potential consequences of harvesting acorns by knocking them from the trees rather than picking them from the ground are numerous. Some Californian ethnographies report this as a rather destructive process (see 3.2.1.3.1.), with twigs and branches broken. In particular, the effects on the next year's production of two-year oaks, which at the time of harvest would bear immature acorns, seem likely to have been potentially severe. Apparently, though, all species were beaten to shake down acorns. It is possible that any losses resulting from damage would be counteracted by the benefits of an increase in light reaching undamaged parts of the canopy, and perhaps even by thinning of immature acorns on two-year oaks, so that such practices could have an effect similar to crude pruning. As far as it is possible to ascertain from the ethnographic literature, such apparently destructive activities do not appear to have adversely affected the availability of acorns.

There may be different consequences of harvesting acorns by knocking them from the trees than of collecting them from the ground after they have fallen. Reduction in competition from ground-feeding competitors, and the ability to obtain the maximum potential crop from one tree are potential advantages of the former method. In densely forested situations with tall, narrow-crowned trees such an option might not be so viable. Some of the potentially significant effects on nutritional qualities and astringency that variation in time of harvesting could have on acorns have been indicated in (6.2.2.2. and 6.4.1.). In particular, harvesting acorns either in an unripe state, or collecting them from the ground after they have been exposed to the weather for some time, could affect the biochemical properties of the acorns. Nutritional differences between acorns which fall from the tree when beaten and those which fall naturally are likely to be small (see 6.4.1.), though these might be significant for those acorns which were actually picked or cut from the trees, as seems sometimes to have been the case in California (see 3.2.1.3.1.). Any nutritional disadvantages of harvesting acorns slightly under-ripe might be counteracted by other advantages. There are some indications in the ethnographic literature (see 3.2.1.3.5.) that "green" acorns may have been particularly favoured for storage, though whether this is because they actually store better, or because they are less good when eaten immediately, is uncertain. Animals which store acorns are generally arboreal feeders, and presumably will be storing slightly under-ripe acorns, so the former may be the case.

8.1.2.3.2. Storage

Because acorns seem to have been thoroughly dried once harvested, effectively killing the seed, it is unlikely that many metabolic changes occurred during storage. The one exception to this is in the case of tannins, which seem to diminish both as acorns ripen, and perhaps over time in storage, as suggested by both the biological (see 6.4.1.; also Puntambekar and Varma 1934) and ethnographic literature (see 3.2.6.3.; 6.5.; also Gifford 1932a). This may be partly because of complexing of tannins with proteins during drying (Harborne1984; Servello *et al.* 1987), forming water-insoluble compounds, which would presumably have the effect of diminishing protein availability from the acorns. To what extent rainfall could enter either storage granaries or particularly storage pits, and leach away nutrients or tannins is unknown. Storage granaries in California seem to have been made watertight as far as possible.

Various studies, including those of Kay (1986), Hilliard (1980), Lopinot (1982), and Petruso and Wickens (1984) have suggested that parching of acorns could be an essential precursor to storage, as it would serve to kill any insect larvae inside acorns. Hilliard (1980) stored acorns for three to four weeks "without parching" to examine destruction of acorn cotyledons and discovered significant damage after this relatively short period. It is unclear, however, whether the acorns were first dried or were kept relatively moist. Work by Winston (1956) has suggested that moisture in the acorn is one of the major limiting factors on infestation by other organisms; and casual observations by the present author suggest that weevil larvae will often leave drying acorns, perhaps because a hardening and drying cotyledon is no longer a suitable habitat. However, it is at approximately this time that larvae will leave the acorn in any case, to pupate (see Appendix 4, 4.2.2.). Certainly the ethnographic record from both eastern North America and California, as well as other regions, suggests that the need to roast or parch acorns to prevent insect activity does not seem to be commonly felt. There may be disadvantages to parching. Petruso and Wickens (1984) experimentally parched acorns before processing them. They found that, apart from killing insect larvae and reducing growth of mould during storage, acorn shells were more brittle and easy to split (see also Hilliard 1980), the testa was easier to remove, and the cotyledon was hardened and more likely to remain whole during shelling. Astringency of the acorns was also reduced, and the taste improved. However, the cotyledons were hardened "to a degree that makes pulverization and mastication extremely difficult, even when the meats are soaked beforehand" (Petruso and Wickens 1984, 368).

8.1.2.3.3. Processing and cooking

Processing of acorns by parching or in other ways might have nutritional or other consequences. Basgall (1987) and Mayer (1976) have suggested that California Indians appear to have used warm water more commonly for those species high in fats (which also seem to be high in tannins, see 6.2.2.2. and 7.4.6.). Mayer suggested that the advantages of using warm water to extract tannins quickly may only be acceptable in the case of acorns which are "nutritionally superior" to begin with. Basgall (1987) also notes the higher labour costs involved in heating water for such processing. Many complex factors have to be examined when considering the relative costs and benefits of different processing techniques. Processing of whole or roughly pounded acorns by boiling, often followed by discarding of the water or rinsing of the acorns, practiced in eastern North America, might result in the loss of considerable quantities of fats or other nutrients. However, the saving in time taken up by fine pounding of acorns, apparently essential for the Californian leaching method, may have made up for any nutritional losses. To what extent the relative availability of fuel, or of utensils for boiling in, especially in the east where metal cooking pots may have facilitated this, is another area of interest. Fernald and Kinsey (1958) noted that in boiling or long soaking much of the sugar is removed from acorn flour, suggesting that some leaching processes could have adverse effects on the natural sweetnesss which, as suggested in 6.5., might counter some of the astringency due to tannins.

Stahl (1989) has pointed out that most models which discuss plant-food processing have viewed it as a source of nutrient loss, as well as treating processing costs as fixed in relation to a particular resource. This seems to have been the case in models of acorn use, as indicated in 8.1.2.1. Stahl points out that resources can often be processed in several different ways, and these might confer certain benefits, as well as have differing costs. Few data are available which have compared the nutritional value of acorns processed in different ways, though Table 8 includes some analyses which have been made at some stages of preparation - for example, on leached and unleached flour, or as comparisons of flour and acorn bread (see also Gaussen and Rouquette 1949; Hilliard 1980; Mayer 1976). Johns and Duquette (1991) have carried out experimental work on the effects on tannin availability of the addition of clay to acorn "bread", as recorded in both California and Sardinia (see 3.2.1.3.6.4.; 3.2.5.3.2.). The effects of using a lye solution in processing, a common procedure in ethnographic accounts from eastern North America, could also be examined. Work on tannins has suggested that their ability to precipitate proteins is lower at high pH (Hagerman and Klucher 1986; Harborne 1982), and Bainbridge (1987) has suggested that the use of lye might have other beneficial effects such as increasing the availability of niacin as it is known to do in the case of maize procesing. Bainbridge and Felger (1989) also suggest that cooking with lye would increase the calcium present in the

finished product. If this is the case it is of particular interest, since nuts are generally thought to be rather poor sources of calcium (see 6.2.5.). In particular, the linear programming model of Keene (1981b) characterised nuts as a poor human resource because of their relatively low calcium content, which may in part be because hickory nuts and walnuts were given zero values for calcium in his model (which is certainly not the case - see Bonner 1971, 1974; Havera and Smith 1979). Keene's model did not attempt to account for any of the nutritional losses or gains which might have been introduced by processing. If acorn foods cooked in lye are indeed better sources of calcium Keene's model might have allocated them a rather more important role, and have altered his model predictions.

Acorns of *Q. robur* collected and processed by this author were analysed at several stages, by Dr. Anthony Leeds of the Department of Nutrition and Dietetics, King's College London. Details of the analyses are given in Appendix 1, and the results are included in Table 8. In one processing sequence flour made from acorns of several trees was leached, though not to a completely tannin-free state, and formed into "loaves" - to some of which were added a clay solution - which were baked overnight in a pit oven similar to those described in the Californian ethnographic record. Table 8 indicates that leaching appears to have slightly increased the quantity of protein, which might be expected because tannin which could otherwise bind with protein is removed. The ash content seems to have diminished, suggesting leaching out of minerals; and carbohydrate to have increased, together with a slight increase in caloric value, though it is difficult to suggest any explanation for this. The cooked bread shows a marked diminution in fat content. Bread with clay appears to have decreased in protein content, which contradicts what might be expected if clay is adsorbing tannins and elements within it are complexing with them, as was suggested by Chesnut (1974) and has been supported experimentally by Johns and Duquette (1991). A sample of roasted acorns was also compared with an unroasted sample, and this too produced an increase in proteins, as well as an increase in fats. An explanation for the latter is hard to find, since, if anything, roasting might be expected to decrease fat content, as lipids are heated and become more volatile. Evidently, there is much scope for more work of this nature, involving processing and cooking under more controlled conditions, and involving the replication of samples, to determine if any of the effects of these, and other processes, on the nutritional value of acorns and preparations made from them are consistent or significant.

8.1.3. Summary - the role of modelling in studies of acorns as a human food resource

There are obviously many aspects of modelling involving estimates of costs of using resources, or of those biological factors which may have an effect on their use, which can be of great value. Model s such as that of Reidhead (see 2.2.2.3.1.; 8.1.2.1.), and many others which have drawn upon it (see 2.2.2.3.1.), have been valuable in suggesting that resources which might superficially appear to be more favourable than others may not be, because of the various costs which have to be accounted for. However, many problems with modelling, and in particular the ease with which assumptions creep into such models, has been demonstrated by the discussion above. For instance, Petruso and Wickens (1984) listed acorn tannin-removing techniques recorded in North America "in order of their relative sophistication, from most primitive to most advanced" (*op. cit.* 362): parching or roasting only; immersion or burial, sometimes with boiling or roasting; mixing with ferruginous earth; parching or roasting and boiling; soaking in fresh water, in sandy depressions, basins, baskets, or pots; boiling only, in fresh water, in pots or baskets; soaking in ash-treated water, and boiling in ash-treated water. They do not explain how they arrived at this ordering, and it would be easy to place the list in many different, but equally arbitrary, orders. Reidhead's decision to include what he assumed to be the most cost-effective method of leaching (see 8.1.2.1.) seems similarly to have missed the point. The role of modelling should be to determine and compare the actual costs of different methods, rather than to assume any differences. It is unfortunate that more experimental work on collection, processing, or other aspects of use has not been undertaken, which might enable more accurate characterisation of such costs. The aim should be to use experimental work and modelling to examine whether assumptions such as the relative efficiency of different methods, or the characterisation of particular resources as preferable to people, are supportable, rather than to build models around such assumptions.

8.2. RELATING MODELS TO THE ARCHAEOBOTANICAL RECORD

8.2.1. Biases in remains and interpretations

So far problems of relating resource models to the archaeological record have not been fully discussed. The extent to which different models have attempted to do this, or thought it possible, varies (see 2.2.1.4.; 2.2.2.3.; 2.2.3.2.; 2.2.4.3.; 2.2.5.3.; 2.2.6.3.). A major problem is that factors such as those of differential preservation, have affected the archaeobotanical record of acorns, as they do for all plant remains. Some of the steps which can be undertaken to overcome problems of taphonomic bias have been indicated by the experimental work of Lopinot (1984 - see 2.2.2.2.). Others, e.g., Asch and Asch

(1986), and Flannery (1986 - see 2.2.3.2.) have expressed doubt about the likelihood of being able to correct for all the biases in archaeobotanical material, and it is perhaps the admitted improbability of being able to do so that has prevented further work being undertaken, even for areas such as those examined by Lopinot, where experiment can potentially aid in understanding.

The need for a more considered approach to interpreting the archaeobotanical record can be demonstrated by some of the statements that have been made, often in more general literature, and especially from Europe, about acorn use based on their presence in sites. Lewthwaite (1986, 60) has mentioned "collecting acorns" as an important part of the economy in the Mesolithic at Grotta dell'Uzzo, Sicily, a site where only two carbonised acorn cotyledons have been recovered (Costantini 1981). Maisels (1990, 80) mentions that "acorns were used" at Beidha, citing Helbaek's (1966) report on plant remains, where the finds constituted one acorn impression in clay. Many other examples can be found in general texts including acorns as part of the economy where sometimes as little as one acorn has been recovered (see, e.g., Phillips 1975). Lewthwaite (1982) suggested a rise in the consumption of acorns during the 3rd and 5th millennia b.c. in parts of the western Mediterranean, based on the number of sites on which this often poor evidence of acorns is found. Both Lewthwaite (1982) and Vencl (1985) have suggested that acorns were not an important Mesolithic food source in Europe, and instead constituted an element of the "Neolithic economy", based on the paucity of Mesolithic acorn finds. The fact that the most likely explanation for this is the paucity of archaeobotanical recovery of any kind from European Mesolithic sites has already been discussed in 2.2.4.2. Donahue (1992, 77) cites Lewthwaite's (1982) conclusions, and suggests that "the California model of intensive acorn (or other nut) gathering is not valid for Mediterranean Europe". The extent of systematic recovery of plant remains, and the scattered record of acorn use in Europe, is a rather poor basis on which to make such statements. The evidence is simply not sufficient to detect temporal trends, or to support or disprove such definite statements as that of Donahue.

8.2.2. Integrating biological, ethnographic and archaeological data - a speculative example

A closer examination of some of the differences in the archaeobotanical record of acorn finds, especially between the different regions which have been considered is of interest, as it demonstrates some of the biases which may be in operation. The most striking difference is in the nature of charred material in eastern North America in comparison with other regions. Since recovery of plant remains in general is especially poor from many of these regions (California, Mexico, eastern Asia, Japan) the comparison with western Eurasia is

likely to be the most revealing. Though there do exist finds of whole charred acorns in eastern North America (see 2.2.2.1.; also Fenton 1978), the majority of remains are of small fragments of shell, and to a lesser extent cotyledon. Such finds do not appear to be recovered from sites in Europe, the Mediterranean, and Southwest Asia, where remains almost always consist of more-or-less whole acorns or cotyledons.

Is it possible to explain the difference between acorn finds in the two regions in terms of taphonomy, either relating to physical differences in the acorns, or differences in the way they were used? European acorns are biochemically most similar to those of the North American white-oak group (see Chapter 6). Lopinot (1984) conducted charring experiments on cotyledons of nuts including one white-oak species (*Q. alba*) and two red-oak species (*Q. rubra* and *Q. velutina*). He examined both the reduction in weight, and fragmentation, occurring during charring. *Q. alba* exhibited the least reduction in mass, with *Q. rubra* slightly more, and *Q. velutina* considerably more. This coincides with Lopinot's general conclusion that nuts high in fats were damaged in this way more than those low in fat. Kernels of white oaks appeared to fragment slightly more during charring than those of red oaks, and it is uncertain to what extent this might cancel out the effects of lower weight loss. Neither do the available data provide any indications regarding post-charring survivability. However, if Eurasian acorns behave similarly to North American white-oak acorns on charring, though there might be a relatively high fragmentation rate, there is no reason to suppose that this would prevent their survival and subsequent recovery.

Shell Thickness (approx.)	Species	Region
Thin c. 0.5mm	*Q. infectoria ssp. boissieri*	Turkey
	Q. faginea	Iberia
	Q. pyrenaica	Southwest Europe
	Q. robur	Eurasia
	Q. suber	W. Mediterranean
Slightly thicker	*Q. alba*	Eastern North America
	Q. brantii	Turkey, W. Iran
	Q. ilex	Circum-Mediterranean
	Q. lobata	California
	Q. macrocarpa	Eastern North America
Medium	*Q. alba*	Eastern North America
	Q. coccifera	S. Europe, Turkey
	Q. rubra	Eastern North America
	Q. velutina	Eastern North America
Thick	*Q. brantii*	Turkey, W. Iran
	Q. ithaburensis ssp. macrolepis	Southeast Europe, Western Turkey
	Q. macrocarpa	Eastern North America
Thickest - max. c. 2mm	*Lithocarpus densiflorus*	California

Table 6. Ranking of North American and Western Eurasian acorns by shell thickness

The survivability of acorn shell must also be considered. Lopinot (1984) found markedly higher mass reduction and fragmentation for the generally thinner shells of *Q. alba* than for the thicker shells of *Q. rubra* and *Q. velutina.* Few comparative data are available on differences in shell thickness between species, either within or between regions. A comparison by eye was made of samples in this author's reference collection, enabling a rough ranking of species on shell thickness, shown in Table 6. The data presented should be treated with caution: considerable variability within species is evident from the range shown by *Q. alba*, *Q. brantii*, and *Q. macrocarpa*, and it is very likely that similar degrees of variation could exist in other species. The data are subjective; and in any case shell thickness may not necessarily relate to shell density or other factors which might be of more importance in survivability. Table 6, does, however, indicate that at least some Eurasian species equal or exceed the shell thickness of North American species, and might therefore be expected to survive in a similar way.

The second approach to explaining differences in the type of acorn finds between eastern North America and western Eurasia involves examining the ways in which acorns may have been used, and consideration of how the acorns became charred. Information pertinent to this question is difficult to find in the ethnographic record, but it is possible to say something about the more likely mechanisms. Finds of charred acorns have been commonly interpreted in Europe as the results of a roasting processing stage gone wrong (see 2.2.4.2.). Such a stage in processing is not commonly recorded in the ethnographic record, though there are some examples. The roasting of acorns seems to have been most common for those species which are relatively sweet, or were eaten in small quantities, as a snack food or delicacy to be eaten immediately, analogous with the roasting of chestnuts. If accidents during roasting of acorns were the only means for charred acorns to enter the archaeological record, the ethnographic data suggest that, paradoxically, charred remains would be more common from sites where acorns were a less important element of the diet.

In North America archaeologists have suggested the use of parching or roasting prior to storage (see 8.1.2.3.2.), with subsequent opportunity for accidental charring. Drying of acorns over or near a fire provides a further way for acorns to become charred, as, for instance, drying racks might collapse. The use of fire for this purpose is reported from eastern North America, but does not seem to have been common in California. It is possible that the generally drier autumn climate here meant that fire was not usually required. If this is an adequate explanation, then the use of fire might be similarly unneccessary in parts of Europe with similarly dry climate, such as the Mediterranean zone or in parts of Southwest Asia. However, the only ethnographic report of drying acorns for storage from this area derives from southern Spain (see 3.2.5.3.1.). It is not possible to dismiss the use of fire for drying acorns even in drier parts of Eurasia, and certainly not in

the damper parts of northern Europe. It must be emphasised, however, that the need for fire in drying for storage does not seem to have been universal even in humid areas such as eastern North America and Japan.

A final possible means of charring is the deliberate burning of shells and other waste, either as fuel, or as a result of disposal of debris on the fire. The ethnographic record includes almost no information about the usual fate of acorn shells, though in one case they are reported to have been considered good fuel, and used as such (see 3.2.1.3.6.1.). Shell fragments are particularly common on eastern North American sites, and rare in Eurasian sites. Differences in site organisation and structures may relate to the way in which waste is discarded, so that the apparently relatively temporary occupations of hunter-gatherer sites on which acorns are commonly found in the eastern United States should perhaps not be expected to be comparable with more permanent village sites in Eurasia. However, many Eurasian sites, especially of earlier periods, could be expected to bear such a comparison.

If the differences in the nature of acorn finds between eastern North America and Eurasia are to be explained by differences in their methods of use it is necessary to account for differences affecting both shells and cotyledons. The absence of acorn shell on sites could be explained by suggesting that disposal as fuel or waste onto fires did not occur, if all charred remains derive from processing waste. However, if acorns were dried, parched, or roasted using fire, this would be likely to result in accidental charring. These processes are recorded ethnographically to have occurred most commonly while shells remained on the acorns, though this need not necessarily always be the case. It would have to be assumed that acorns in Eurasia never came near fire until after their shells had been removed. The absence of cotyledon fragments could be explained by assuming that acorns were either never brought near fire except whole, which the ethnographic evidence, for example from Sardinia, suggests is unlikely to have been the case; as well as that whole acorns never became fragmented during or after charring. The improbability of all these conditions always being met throughout the whole area and period under consideration, together with the need to explain lack of survival of any such fragments due to greater delicacy than those of eastern North America, suggests that a rather more parsimonious explanation may be called for.

Obviously, the simplest explanation is that acorns were not, or were very infrequently, used in Eurasia. However, this does not seem to be the case, since, as has been pointed out, whole or large fragments of charred acorns have been recovered from sites. On older sites especially, lack of preservation might be postulated as an explanation. In Southwest Asia charred acorns have been found at the site of Ohalo II, dating to 19000 B.P. (see 2.2.5.1.). In Japan acorn finds date to the earliest part of the Jomon, c. 13000 - 9500 B.P.

(Koyama 1978), and in eastern North America charred remains of nuts, including acorns, date to the early Archaic, e.g., in levels radiocarbon dated to c. 8350 and c. 7600 B.P. at Campbell Hollow (Asch and Asch 1985a) and c. 7155 B.P. at Koster). In all cases acorn finds are roughly contemporaneous with the earliest reported plant remains, so there is no reason to suppose that acorn finds should be biased against by the age of a site.

Many Eurasian sites at which recovery of whole acorns is recorded were excavated before the introduction of flotation or other systematic recovery of plant remains, in some cases during the last century, and it is not surprising that small fragmentary remains are not recorded. Sites excavated more recently however, using systematic recovery techniques, would be expected to produce similar results to North American sites, and it is possible that fragments of shell and cotyledon have been "lost" somewhere between recovery and identification. The likely very small size of shell and cotyledon fragments (again by analogy with eastern North American finds), together with the amorphous appearance of cotyledon fragments, combined with the focus by archaeobotanists on morphologically-recognisable remains such as seeds, suggest that this is not unlikely. Analogies with the recovery and recognition of charred vegetative parenchyma (Hather 1991), and work being undertaken by colleagues at the Institute of Archaeology, suggest that once the possibility of both recovering and identifying such amorphous and fragmentary material has been demonstrated, the material miraculously begins to appear on archaeological sites. In one case such material has been recovered from the Bronze Age site of Peñalosa, in Andalucia, southern Spain, and is in the process of identification, using anatomical characters recognisable using scanning electron microscopy. As well as vegetative parenchyma there are fragmentary remains of other tissues, ranging in size, but including many fragments as small as 2mm across, of what appear, by comparison with modern experimentally-charred material, and morphologically-recognisable material from the site, to be acorn cotyledon (L. Peña Chocarro pers. comm.).

One further point requires consideration. If acorn fragments are not, or rarely, recovered from European sites, why are hazelnut shell fragments so common? Lopinot's (1984) experimental work again provides some possible indications. He found that hazelnut shell showed mass reduction during charring intermediate between that of acorns and of thicker-shelled nuts such as hickory, and commented that the shell "was surprisingly resistant to carbonizational fragmentation" (*op. cit.*, 135). It is potentially dangerous of course, to extrapolate such findings to a different species of hazel, and different species of acorns, but the indications are that hazelnut shell is likely to survive charring processes rather better than is acorn shell. Also relevant in this respect is the comment of Legge (1989, 219) that "pieces of hazel-nut shell are .... large enough to be found even with the trowel and by dry sieving".

8.2.3. Prospects for future work in modelling the role of acorns in human subsistence

The lines of argument used above are of course rather speculative, and deal with a very generalised question, to which the answer may in any case have seemed rather obvious. Nevertheless, they illustrate something of the way in which the three major lines of evidence which have been discussed in this study - the archaeological, the biological, and the ethnographic - can be brought together in discussing the potential role of acorns in human subsistence. They also point towards some of the ways in which the hypothesis outlined could be further examined, or tested. As acorns are almost invariably compared with hazelnuts in Europe, a fuller investigation of the ethnographic record of hazelnuts might also provide useful indications with regard to their apparent abundance on many European archaeological sites. In comparison with eastern North America, the northern European nut flora at least, is poor in species. Very few studies like those undertaken in North America, and to a lesser extent Japan, of relative yields, and those other biological characteristics which could affect availability of resources to people have been undertaken in Eurasia. Though, as has been pointed out above (8.1.1.), such studies are fraught with difficulties, fuller investigation could potentially provide useful indications. An experimental investigation of the effects of charring on European acorns, particularly in comparison with the effects on European hazel nuts, and ideally including other commonly found subsistence remains, such as cereals, could provide useful information. Archaeobotanical samples, especially those recovered by flotation from sites where there is already evidence of acorns, should be re-examined for very small fragmentary remains. The need for further experimental work, on determining cryptic characters which could aid in the identification of both very small shell fragments, and of the fragments of non-vegetative parenchyma such as that which constitutes the bulk of the acorn, is also indicated.

The fact that problems of preservation, recovery, and recognition, especially of fragmentary acorn remains, are likely to be of importance means that the archaeological record of acorn use is difficult to accept at face value. This is undoubtedly a problem with archaeobotanical research in general, but until such biases can be accounted for, or at least acknowledged more explicitly, it means that attempts to examine subsistence remains and determine their implications for the past history of subsistence may often be meaningless.

8.3. ACORNS AND THE ROLE OF WILD PLANTS IN PAST HUMAN SUBSISTENCE

Taphonomy is not the only bias affecting interpretations of the archaeological record. As has been demonstrated in Chapter 2 and 8.2.above, the archaeological data on acorns vary considerably between the regions which have been discussed. The interpretations made regarding acorn use also vary, but it is often difficult to see how these variations relate to the archaeological, and certainly the archaeobotanical record. For example, in both California where finds of acorns have been small (though processing technology associated ethnographically with their use exists), and Japan, where many acorns that have been found are waterlogged, and of doubtful cultural origin (Crawford 1983), acorns have been inferred to have been a major element of past diet. A similar paucity of finds on similar hunter-gatherer sites in western Eurasia has not been interpreted in such a way. In California and Japan the use of acorns as an important, even esteemed, food, is recorded historically. In western Eurasia the historical and ethnographic record generally characterises acorns as a famine food, or one eaten only by poorer sector's of the population. It may be that this characterisation is largely responsible for the unwillingness, in Europe particularly, of archaeologists to consider the possibility that acorns (or indeed other plants) may have been important Mesolithic foods. Certainly there is little more direct evidence for acorn exploitation in Californian and Japanese "hunter-gatherer" sites than there is in Eurasia.

Attempts to rationalise this view of the unimportance of wild plant foods in the European Mesolithic have drawn on their supposed unsuitability as food resources. Rowley-Conwy (1984a, 307), for instance, has suggested that storage of hazelnuts, prolonging their period of use and enabling them to constitute a more important food resource, might have been difficult in mesolithic Denmark, since " if they are collected when thoroughly ripe, correctly dried, stored in a suitable container, covered with a layer of sand, and kept in a cool cellar, they may last until late March. The unlikelihood of all these conditions being met in the Ertebølle would certainly raise the risk of spoilage before this". The potential technical capabilities of past populations are frequently underestimated by archaeologists, and in no field more than that of the storage of plant materials. Storage of plant foods by hunter-gatherers and similar populations (such as the eastern North American Indians) of a remarkable range of foods is actually recorded in the ethnographic record. While small seeds, and perhaps nuts, are considered to have been most amenable to storage, there are numerous records of preservation and storage of plants using "traditional" methods, of foods ranging from roots and tubers, through soft fleshy fruits, to leaves (see, e.g., Balls 1962; Barrett and Gifford 1933; Densmore 1974; Gilmore 1919; Smith 1932; Swanton 1946; Yanovsky 1936). In addition, there is ample ethnographic evidence for storage of

hazelnuts in areas such as the wet Pacific west coast and eastern North America (Du Bois 1935; Gunther 1973; Kniffen 1939; Smith 1923), and of other nuts, especially acorns (see 3.2.2.2.2.; also Lopinot 1982).

The difficulty of storage of hazelnuts has been reiterated for Neolithic Britain by Legge (1989, 219), who in addition notes that "the indications that we have suggest that nuts are not a highly efficient food resource for large scale use", citing Keene's (1981) model of eastern North American nut use, and its characterisation of them as low-ranking resources, which as discussed elsewhere may be questionable. Acorns recovered from "post-agricultural" Eurasian sites have generally been interpreted as an important supplementary resource gathered by agriculturalists, usually at times of food scarcity. The role of wild plants is not considered to have been generally important however, and this view is repeated in other regions, including post-Jomon Japan (strangely, since the ethnographic record there relates largely to people practising agriculture), Mexico, and, to a certain extent, eastern North America. In all cases there has been an emphasis on the domestication and use of agricultural crops, and this has seemingly resulted in a lack of interest in the role of wild food plants. The evidence presented in Chapter 3 suggests to the contrary, that, at least in the case of acorns, and probably in the case of other wild plants, a potentially extremely important aspect of past diet has been largely ignored by archaeobotanists, and that general characterisations of subsistence in the period after the introduction of domesticated plants may need revision.

Models generally may be constrained more by prevailing paradigms than they are by available data. The overwhelming paradigm in the archaeology of subsistence is undoubtedly still that of the "agricultural revolution". The discussions of various regions in Chapter 2 have all demonstrated the lack of interest in plants other than domesticates once the presence of domesticates has been detected. There are signs indicating that this particular paradigm may be about to shift, and the potential role of wild plants, as well as animals, in "agricultural" systems is being increasingly discussed in both the archaeological and ethnobotanical literature (see, e.g., Dolukhanov 1979; Entwistle and Grant 1989; Gregg 1988; Greig 1991; Javier Caballero and Cristina Mapes 1985; Jørgensen 1977; Legge 1989; Messer 1978; Moffet *et al.* 1989; O'Shea 1989; Wilken 1970). Harlan (1989, 9) has written: "today [in Africa], most of the gatherers [of wild plants] are subsistence farmers rather than true hunter-gatherers. Perhaps nothing could show more clearly the non-revolutionary nature of agriculture than this fact. After farming has been fully established for thousands of years, it is still worth the effort to gather food from the bush".

As G. Hillman (pers. comm.) has pointed out the realisation that many wild plants, fruits, nuts, "greens", herbs, etc may have been included in the diet of past agricultural

populations on a regular basis is hardly surprising, since such behaviour has continued, even in a high-technology agricultural and industrial society such as that of Britain, until recent times, and in the case of some resources (e.g., blackberries) to the present day. The evidence of herbals, and the residual knowledge of food and medicinal uses of wild plants still demonstrable in books written for the general public on the subject, implies something of the importance and frequency of use of such plants in previous centuries. The supplementary role of such plants in agricultural societies should be an area of greater interest to archaeologists than it apparently is. What may be of most significance though, is the role that wild plants which could fill the role of a "staple", by substituting nutritionally for the domesticated crops, may have had in past societies.

The ethnographic record discussed in Chapter 3 has shown that through much of the area of their distribution acorns have filled such a role. In the face of the "agricultural revolution" paradigm the role of what is often recorded "merely" as a famine food is seen as one that can be of little importance - what is important is the agricultural crops which supposedly provided most of the energy input to the diet. Again, an examination of the ethnographic and historical record has demonstrated the frequency of recourse to acorns as a "famine" food, as well as its persistence as a regular component of the diet in many areas where agriculture had been practised for thousands of years. Hilliard (1986) and D. Zohary (pers. comm.) have suggested that acorns may have filled an important role during the early stages of agriculture. They have emphasised the similarity of acorns' nutritional and culinary role to that of cereals, their potential abundance and storability, and the fact that their harvest can be scheduled without conflict with agricultural activities, and occurs after cereal harvest, at a time when any shortfalls in agricultural produce would be recognised and could be substituted for by acorn collection. To what extent acorns, or other plant foods which could have performed a similar function, have been regularly resorted to in various places and at various periods in the past, or conversely to what extent they have been used only in times of extreme desperation, should be a problem of particular interest not just to those interested in the use of wild resources, but also to those concerned with the development of systems in which agriculture has played a role in subsistence.

8.4. ACORNS IN SUBSISTENCE AND IMPLICATIONS FOR GENERAL MODELS OF SUBSISTENCE CHANGE

A major aim of this thesis was, as stated in Chapter 1, to examine differences in the use of acorns as they have been incorporated in various subsistence strategies, and to examine the implications of any findings for general models of subsistence change. Certain problems with achieving this aim have been identified during the period of research.

In particular, in using a wide-ranging approach, examining data from many regions, it had been hoped that it would be possible to come to some general conclusions about the ways in which acorns have been used, and about the factors correlated with their use. However, the fact that the quality of information both about acorn use, derived from the ethnographic and archaeological records, and regarding ecological and biological characteristics of acorns, varies enormously, especially between the different regions which have been examined, has made it very difficult to draw other than the most elementary generalisations.

For example, comparisons between regions might have enabled the extent to which there appear similarities in the use of acorns in similar ecosystems to be determined. Are there, for instance, more similarities between patterns of acorn use in California and the Mediterranean, or Japan and eastern North America, than there are between the two types of environment? The sand-basin leaching process, apparently requiring very fine pounding of the acorns, and able to proceed without the need for prolonged boiling of water (except perhaps during the subsequent cooking process), is characteristic of California. Whether a similar technique has ever been used in other areas, particularly the environmentally-similar Mediterranean and Southwest Asian regions, as has been suggested by some, is uncertain. Much of the ethnographic data from these areas are not specific enough to determine the exact ways in which tannins were removed, though some of the reports suggest some similarity with the Californian method. The method apparently characteristic of eastern North America, of boiling acorns in water, sometimes with the addition of lye, appears fairly similar to techniques recorded in Japan. This boiling method is also repeated in some of the examples of acorn processing recorded from the Mediterranean and Southwest Asia, particularly Sardinia. Although there are perhaps therefore detectable patterns in the processing techniques used in certain areas it is difficult to determine whether these can be correlated with environmental or other external factors, or whether these, and differences between areas, are as readily explained as a result of "cultural" factors. Similarly, whether differences in the use of acorns in terms of their culinary and dietary role (for example, as bread-like staples, or as roasted, boiled or raw snacks) can be correlated with other factors, such as the number of different available species present in any locality, is an area that requires further investigation. In the author's opinion the available data do not at the moment enable us to answer such questions definitively, although they may enable us to generate more specific hypotheses in these areas of interest which could be examined further. These might then enable us to hypothesise about techniques or ways of use which may have been used in areas for which there are incomplete records, or in the past.

A more specific question which might have been examined is whether differences in use, in particular in intensity or method of processing, relate to particular nutritional and biochemical characteristics of the species involved. In addition, do the characteristics of

species selected for use relate to the role which acorns play in the overall subsistence pattern - are different types of acorn selected when the food is an occasional or snack food, a "famine" food, or a regular component of diet? In both western North America and the Mediterranean and Southwest Asia, the use of sweet acorns, often eaten roasted like chestnuts, has continued until the present day. This correlation between method of use and acorn type is, however, hardly an unexpected one - it is more difficult to come to general conclusions about acorn type where they have been incorporated in other ways in subsistence. For example, the circum-Mediterranean *Q. ilex*, frequently recorded as having been used throughout its area of distribution, has been treated as both a roasted snack, and as a highly processed carbohydrate foodstuff. This species is variable in its sweetness, and together with taxonomic problems, this makes it difficult to determine whether sweet or more bitter acorns are being used in the intensive and time-consuming processing methods such as that recorded in Sardinia (see 3.2.5.3.2.). In Japan too, very time-consuming and laborious processing seems to have been undertaken with acorns apparently relatively low in tannin (by comparison with many of the North American species - see 3.2.8.2.3., also Tables 8 and 10); and data from western Iran suggest the use of a long leaching process, almost certainly for the relatively sweet acorns of *Q. brantii* (see 3.2.6.2.2.). The data from eastern North America are not generally specific enough regarding species used to determine whether there are significant differences. In California the major difference between processing of acorns of different species, other than in the types of foodstuff for which they might be preferred, seems to have been the length of the leaching period (see 3.2.1.3.6.3.), which sometimes seems, as might be expected, to have been longer for more tannin-rich species. The data from the other regions mentioned above indicate, however, that we should not assume that the intensity of processing necessarily relates directly to the tannin content of the acorns involved. Quite apart from problems with interpreting the ethnographic data, a major difficulty is the poor availability of quantitative, or even good comparative qualitative, data on tannin content, with very little of what does exist being legitimately comparable (see 7.4.1.).

An area of particular interest to those concerned with the history of subsistence is the extent to which any resource can be intensified, or, put simply, its productivity improved. General models of subsistence change imply that increasing intensification of management of a resource should correlate with an increasing, or at least maintained, importance in the overall subsistence strategy. Again, with regard to acorn use, there is little good ethnographic data on intensification of management. As far as we can tell, burning of the areas around oak trees, to facilitate collection, seems to have been the limit of "management" applied to the acorn resource by the Californian Indians, undoubtedly the most intensive known users of acorns. Burning may have reduced disease and increased the speed of nutrient cycling in the vicinity of the trees. It is possible that the breaking of

branches sometimes recorded as a consequence of harvesting may have acted in a similar way to pruning, leading to increased productivity. To what extent there may, at some time, in any area where acorns have been used, have been selection for oaks, either of particular species or of productive individuals, by planting or by selective felling of trees is a question of great interest. If oaks do respond better than many other deciduous genera to disturbance, as some have suggested, and for which there is some support (see 4.6.), then there may have been, from early times, unconscious selection to increase the numbers of oaks present. Whether this would necessarily increase production of acorns is, however, uncertain. Perhaps thinning of regrowth stands and continued clearance of adjacent trees would be necessary to produce the increase in acorn productivity which could be considered as a form of intensification. The extent to which palynological data could be used to distinguish between the presence in the past of open-growth and potentially productive oak woodland, and dense and possibly less productive stands, is an area requiring investigation. The most "intensive" forms of management of oak trees recorded from recent times come from southwestern Iberia, where oaks have been selected and pruned to improve productivity of acorns for pigs (see 3.2.5.2.). The propagation by grafting of particularly sweet trees for human consumption is also recorded from southwestern Europe (see 3.2.5.1.). In other areas, such as southeastern Turkey and many parts of the Mediterranean, oak trees are, or have been, intensively managed for leaf fodder and wood, but it is uncertain to what extent such patterns of management may have been compatible with the production, or intensification of production, of acorns. Again we have to conclude that the data we have are not at the moment sufficient to enable us to produce good generalisations about intensification of the acorn resource, and that further investigation is needed before reliable models can be constructed regarding correlations between management and acorn use in the past. However, we can say that the general data we have appear to contradict the pattern which would tend to be predicted by general models of subsistence intensification, i.e., that the more intensive forms of management are likely to correlate with the most intensive use of the resource.

Generally then, attempting to compare between regions, and producing a reliable comparative summary of the use of acorns throughout the area of their distribution is made extremely difficult by the patchy nature of the available data. In addition, the author has been made particularly aware, by a detailed examination of the attempts which <u>have</u> been made in the literature, of the pitfalls of attempting to model the role of acorns, using incomplete data from a combination of the fields of archaeology, ethnography, and the biology of oaks and acorns. The author recognises that, by the nature of the process, the use of incomplete data is inevitable when attempting to model the probable past role of a resource, but, in view of the incompleteness of, and difficulties which have been identified with, the data, and the often biased, and not always explicitly expressed, assumptions

which are consequently incorporated in many models, feels there is a need to question the utility of much modelling in advancing our understanding of past human subsistence.

The explicit use of models in archaeology is something which has arisen in conjunction with attempts to transform archaeology into a scientific discipline. Unfortunately, many in the field have adopted the use of modelling, especially that involving quantification, in the apparent belief that this, together with the use of data obtained with scientific techniques, in itself constitutes a scientific approach. It is unfortunate that the application of a scientific methodology has not been so eagerly seized upon. The author certainly believes that modelling can play a role in helping to understand past human subsistence, but feels that the role of modelling in relation to archaeological investigations in this particular field needs to be fundamentally reassessed. Many of the reasons for this in relation to acorns, and suggestions regarding ways in which modelling could contribute to our understanding, in perhaps more modest, but more practicable, ways have been discussed in sections 8.1. and 8.2. In the author's opinion, it is only when a more fundamental understanding of the resources we are examining, and the effects of the activities which can be involved in their utilisation, have been realised, that we can hope to approach questions regarding such things as determining cross-regional (or -cultural) common denominators in processing techniques or the extent to which there are differences between the use of acorns within different subsistence systems, and to approach "higher level" questions, such as that of intensification, of interest to those concerned with the history of subsistence and subsistence change.

Given these reservations, however, it is of interest to examine more closely Harris' (1989) general model of subsistence intensification, referred to in Chapter 1, and reproduced below. As the discussion of intensification above has suggested, there are difficulties in attempting to relate our understanding of the roles of acorns to such a model. This is partlybecause the model is implicitly based upon those plant types which can be shown to be used at all stages along the continuum of development in plant-human interactions, from wild plants obtained by foraging to domesticated plants obtained by farming - particularly the cereals and root crops, and their wild relatives or analogues. Certain elements of the model, therefore, particularly those which emphasise the importance of tillage, are probably of little relevance to tree crops such as acorns. Another problem is in distinguishing between intensification of a subsistence system as a whole, and intensification of individual resources within systems. Thus acorns, as the ethnographic record demonstrates, can be incorporated <u>within</u> any of the "food-yielding systems" from wild plant-food procurement to agriculture, though within the latter the acorns themselves may constitute a virtually unmanaged resource (e.g., as a "famine food") with few "plant-exploitative activities" applied to the trees; or alternatively they may be a relatively intensively managed and prop-

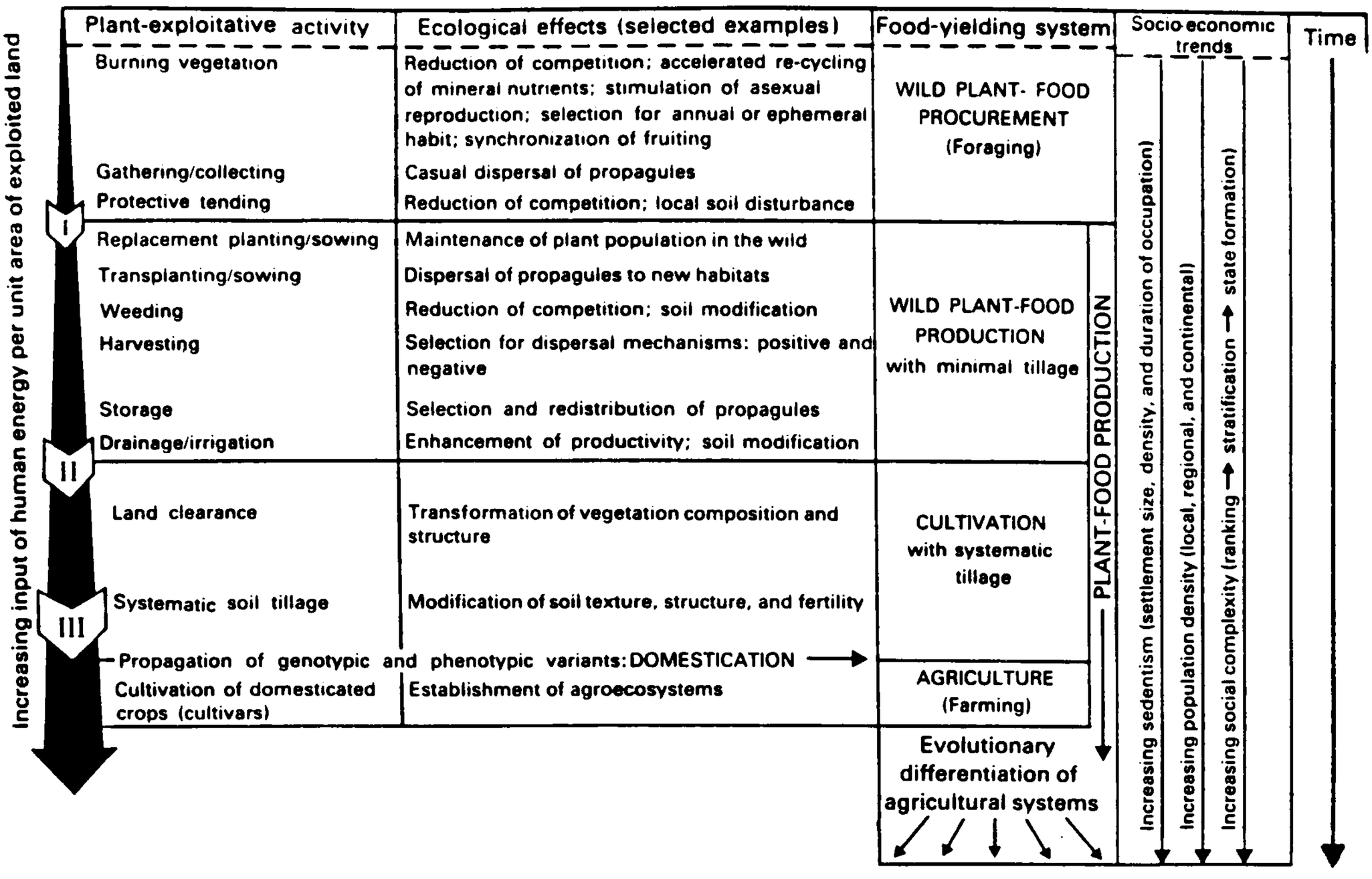


Figure showing "evolutionary continuum of people-plant interaction", reproduced by permission from Fig. 1.1. in D.R. Harris and G.C. Hillman: *Foraging and Farming: The Evolution of Plant Exploitation* (the Roman numerals indicate postulated energy thresholds)

agated, perhaps even a domesticated, resource, though perhaps of little dietary importance (e.g., as a chestnut-like roasted snack). It is difficult to determine how to fit ethnographic examples into the categories of wild plant-food procurement and wild plant-food production. As discussed above, as far as we are able to tell from the ethnographic data, the California Indians were carrying out few "plant-exploitative activities" other than burning, gathering/collecting or harvesting (the distinction is not clear with respect to acorns) and storage. The last two of these are included within the wild plant-food production food-yielding system division of the continuum, but it would be difficult to argue that the available examples demonstrate food-production rather than food-procurement.

The partial answer to most of these problems lies in the point made by Harris (1989, 18) that the gathering of wild plants may persist in "developed agroecosystems", and that activities from earlier stages of the continuum will be included at later stages; as well as his emphasis that the model should not be taken to be unidirectional (op. cit., p.12). Additionally, the model was developed explicitly to clarify understanding of the emergence of agriculture (p.22). Nevertheless, there are important points raised by the difficulties shown in relating the model to the use of acorns, usually a wild resource which, though probably nowhere achieving the position of a truly "agricultural" crop as defined by the model, may have approached this in terms of selection for, or even propagation of, genotypic and phenotypic variants. Perhaps most important of these is the fact that the

model, as do most models of subsistence change, places a great deal of emphasis on those few plants which have become agricultural crops, an area of undoubted interest, but one which, as pointed out in section 8.3., has tended to detract from the consideration of, or investigation by, those interested in the history of subsistence, of the sometimes vitally important role that other plants have played.

CHAPTER 9. SUMMARY CONCLUSIONS

This thesis has examined some of the constraints on interpretation of the possible role of acorns in past human subsistence from several disparate areas of research, including the archaeological evidence, the ethnographic record, and information on the biological and ecological characteristics of acorns and oak trees.

The available data of all kinds vary greatly among those parts of the world in which oaks are found. Thus very little is known about areas such as China and Mexico, whereas a considerable amount of information is available about North America.

The review of the archaeological evidence for the use of acorns, and the way it has been interpreted, indicated that there are differences in both the archaeological record and the methods and sophistication of interpretation applied, especially between different regions. It is therefore very difficult to compare region with region on a meaningful basis. In addition it is difficult to say whether apparent differences over time and space are due as much to real differences in the use of acorns in the past as they are to the differing levels of recovery, analysis and interpretation.

The ethnographic data also vary considerably in quality from region to region, as does the way they have been used in interpreting the possible past role of acorns. Though ethnography has been implicitly accepted as having some relevance in the interpretation of the archaeological record of acorn use, it is often used in a rather generalised way, in the form of simple analogies, often based on the more well-known studies; and without explicit consideration of the archaeological implications of the way in which these examples are being used as "models". Not only does the ethnographic record provide several potential "models", but the variability present in the ethnographic record is rarely reflected in archaeological discussions, and the extent to which different ethnographic models might result in the same archaeological results is rarely considered.

Some models have attempted to characterise the acorn resource in terms of factors such as productivity, or costs and benefits of use, often drawing upon the biological literature. The discussion of models which have attempted to characterise acorn resources in certain ways has illustrated some of the problems with the use of such data, and with their application to the past role of acorns, as well as the types of assumptions that have been made by archaeologists relating to the characteristics of acorn resources.

Resource models in general are often used once and are not applied to, or tested in, different areas on different sets of data; nor are their implications often tested against archaeological data; nor are the predictions of several alternative models tested against each other. If resource models are to be a useful aid in interpreting the past then it is necessary for them to examine the effects of different assumptions, and to compare different methods of using resources. The need for a greater understanding of, and more critical approach to, the available data - archaeological, ethnographic, and biological - is clear.

The importance of critically combining data from all these areas of study has been demonstrated in the discussion of the problems and potential for modelling the role of acorns in past subsistence. In addition, the value of a detailed examination of one potential food resource has perhaps been demonstrated most clearly by the insights this has generated into problems with a more wide-ranging relevance. In particular, the implications regarding the potential importance of the role of wild-plant resources, not just in hunter-gatherer subsistence, but also in subsistence systems in which domesticated plants play a role, has been emphasised. This study has also demonstrated that one of the major constraints on any interpretations are preconceptions about the likely role that acorns, or other wild resources, could have played in the past.

APPENDIX 1. NUTRITIONAL DATA - TABLES

1.1. NOTES TO NUTRITION TABLES

Figures are for acorns (or nuts) minus their shells, except where indicated. Figures are expressed as % of dry weight; except those for moisture, which are as % of acorn weight prior to analysis.

Energy values are in kJ/g of dry weight.

Tannins are analysed separately, and presented as % of dry weight.

Protein is crude protein, fats are ether extracts, carbohydrates are nitrogen-free extract, except where otherwise indicated as follows:

1 - crude fat/fats/lipids/oils not specified as ether extract

2 - "carbohydrate"

3 - "available carbohydrate"

4 - "soluble carbohydrate"

5 - "total carbohydrate"

6 - carbohydrate by difference

7. - source in which value of nitrogen only was given: in these cases the value was multiplied by 6.25 to obtain the protein value (Paul and Southgate 1978).

Energy values were derived by calculation from proximate constituents, applying conversion factors to the values given for protein: 17 kJ/g, fat: 37 kJ/g, carbohydrate: 16 kJ/g (Holland *et al.* 1991). Fibre values, where provided separately, have been excluded from the carbohydrate figure, as these represent an indigestible portion (Holland *et al.* 1991, Paul & Southgate 1978).

Other figures, shown in [ ] are:

8 - energy value as given in indicated source (in most cases recalculated to kJ/g using formula kJ/g = cal/g x 4.184 (Holland *et al.* 1991)

9 - energy value determined by bomb calorimetry (recalculated to kJ/g as above where necessary)

10 - samples from own reference collection submitted for analysis to Dr. Anthony Leeds, Department of Nutrition and Dietetics, King's College London, in November 1991. Sample sources and dates of collection are given. Shells, and testas as far as possible, were excluded. Some samples were of material previously processed, as indicated. Samples generally consisted of 50g or more of material. Analytical methods used were:

Protein - from determination of nitrogen by the Kjeldahl method, multiplied by 6.25.

Fat - ether extraction by the chloroform methanol extraction method.

Ash - dry ashing in furnace.

Carbohydrate - by difference.

Energy - metabolizable energy by Ballistic Bomb Calorimetry.

Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
1. Western North America									
Hippocastanaceae									
Aesculus californica (inc. shell)	64.7	8.2	1.3[1]	81.8	5.0	3.9	15.0	—	Wolf 1945
Pinaceae									
Pinus cembroides var. *edulis*	3.1	13.4	62.4	20.0[2]	1.1	3.0	28.6 [27.3[8]]	—	Watt & Merrill 1963
P. edulis	3.4	15.1	64.1	17.9[5]	—	2.9	29.1	—	Winton & Winton 1932
P. monophylla	2.2	3.9	36.2	15.6[2]	—	—	16.6	—	Heizer & Elsasser 1980
	3.8	6.8	63.1	27.2[5]	—	2.9	28.9	—	Winton & Winton 1932
P. sabiniana	5.1	29.6	56.6	8.9[5]	—	5.0	27.4	—	"
Pinus sp (nut butter)	6.7	14.0[7]	58.3	—	—	—	[26.4[8]]	—	Carpenter & Steggerda 1939
	6.0	11.3[7]	25.5	—	—	—	[23.0[8]]	—	"
2. Eastern North America									
Corylaceae									
Corylus americana	2.6	26.5	61.4	7.2	2.2	2.8	28.4	—	Wainio & Forbes 1941
Corylus sp. (inc. shell)	6.0	6.7	20.5	19.3	52.0	1.5	11.8	—	King & McClure 1944
Fagaceae									
Castanea dentata	34.5	12.2	16.4	65.1	3.6	2.6	18.6	—	Winton & Winton 1932
	4.8	12.2	16.1	66.2	2.8	2.7	18.6	—	"
	33.5	15.3	15.3	63.8	2.9	2.9	18.5	—	"
Fagus grandifolia	—	7.8	10.6[1]	6.5[5]	—	—	6.3	—	Bonner 1974
	4.0	22.8	59.8	13.8[5]	—	3.6	28.2	—	Winton & Winton 1932
Hippocastanaceae									
Aesculus glabra	52.7	12.6	6.1	74.0	2.5	4.8	16.2	—	Wainio & Forbes 1941
A. pavia (whole seed)	—	8.2	1.9[1]	42.9[5]	—	—	9.0	—	Bonner 1971

Table 7. Nutritional data - northern temperate nuts (cont. over)

Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Juglandaceae									
Carya aquatica	16.1	—	—	—	—	—	[25.6[89]]	—	Burns & Viers 1973
C. cordiformis (inc. shell)	—	3.3	30.8[1]	17.1[5]	—	—	14.7	—	Bonner 1974
C. glabra	53.2	—	—	—	—	—	[33.3[89]]	—	Burns & Viers 1973
	—	—	—	—	—	—	[26.5[89]]	—	Lewis 1982
C. illinoensis (wild, inc. shell)	7.5	7.8	18.5[1]	35.0	36.2	2.4	13.8	—	Billingsley & Arner 1970
(inc. shell)	—	9.3	32.8[1]	13.3[5]	—	—	15.8	—	Bonner 1971
	7.0	—	—	—	—	—	[32.9[89]]	—	Burns & Viers 1973
	3.7	10.8	72.5	13.2[2]	1.8	1.8	30.8 [28.4[8]]	0.3	Friedemann 1920 (cited in Asch *et al.* 1972)
	2.7	8.3	74.7	13.2	2.1	1.7	31.2	—	Henry 1950 (cited in Asch *et al.* 1972)
	3.4	12.5	73.2	8.8	3.8	1.7	30.6 [32.1[8]]	—	Howes 1948
	3.4	9.5	73.7[1]	12.7[2]	2.4	1.7	30.9 [29.7[8]]	—	Watt & Merrill 1963
	2.7	9.9	72.5	15.7[5]	—	2.0	31.0	—	Winton & Winton 1932
	3.2	11.4	74.4	10.3	2.3	1.7	31.1	—	"
C. laciniosa (inc. shell)	—	1.6	8.7[1]	13.8[5]	—	—	5.7	—	Bonner 1971
C. leiodermis	49.3	—	—	—	—	—	[25.2[89]]	—	Burns & Viers 1973
C. myristicaeformis (inc. shell)	—	5.8	15.2[1]	16.1[5]	—	—	9.2	—	Bonner 1971
C. ovata	—	12.4	70.6[1]	5.3[2]	—	—	29.1	—	"
(inc. shell)	—	5.9	37.4[1]	13.0[5]	—	—	16.9	—	"
	35.5	—	—	—	—	—	[32.6[89]]	—	Burns & Viers 1973
	—	—	—	—	—	—	[31.6[89]]	—	Havera & Smith 1979
	3.4	11.6	72.7	11.8	2.1	1.8	30.8	—	Peterson & Bailey 1913 (cited in Asch *et al.* 1972)
	—	—	29.3[1]	—	—	—	[27.5[8]]	—	Smith & Follmer 1972
	2.2	13.3	74.4	8.8	1.5	2.0	31.2	0.5	Wainio & Forbes 1941
	3.7	16.0	70.0	11.8[5]	—	2.2	28.7	—	Winton & Winton 1932
	4.0	21.3	67.3	6.7	2.4	2.3	28.6	—	"
	3.5	13.7	72.7	9.7	2.1	1.8	30.8	—	"
C. texana	4.9	—	—	—	—	—	[33.9[89]]	—	Burns & Viers 1973

Table 7. Nutritional data - northern temperate nuts (cont.)

Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
C. tomentosa (inc. shell)	—	3.7	20.0[1]	12.7[5]	—	—	8.2	—	Bonner 1974
	49.3	—	—	—	—	—	[30.9[89]]	—	Burns & Viers 1973
	—	—	—	—	—	—	[30.9[89]]	—	Havera & Smith 1979
Carya sp.	3.3	13.7	71.3[1]	11.3[2]	2.0	2.1	30.5 [29.2[8]]	—	Watt & Merrill 1963
Juglans cinerea	3.8	24.6	63.6[1]	8.7[2]	—	3.0	29.1 [27.3[8]]	—	"
	4.5	29.2	64.1	3.6	—	3.1	28.7	—	Winton & Winton 1932
Juglans nigra	11.0	32.6	37.0	24.9	2.1	3.4	23.2	—	Baumgras 1944
	—	23.1	60.4[1]	3.8[2]	—	—	26.9	—	Bonner 1971
(inc. shell)	—	5.1	10.5[1]	14.4[5]	—	—	7.1	—	"
	—	—	—	—	—	—	[29.4[89]]	—	Havera & Smith 1979
	—	—	23.1[1]	—	—	—	[26.1[8]]	—	Smith & Follmer 1972
	2.9	29.3	60.2	6.7	1.0	2.8	28.3	0.3	Wainio & Forbes 1941
	3.1	21.2	61.2[1]	13.5[2]	1.8	2.4	28.4 [27.1[8]]	—	Watt & Merrill 1963
	2.5	31.1	59.3	5.9	1.6	2.1	28.2	—	Winton & Winton 1932
3. Europe, the Mediterranean and Southwest Asia									
Anacardiaceae									
Pistacia vera	4.2	23.6	56.9	16.3[5]	—	3.2	27.7 [28.3[8]]	—	Howes 1948
	4.4	15.9	63.6	16.3	1.4	2.8	28.8 [29.4[8]]	—	Kuzayli *et al.* 1966
	5.3	20.4	56.7[1]	18.1[2]	2.0	2.9	27.3 [26.3[8]]	—	Watt & Merrill 1963
	4.2	23.3	56.4	17.0[5]	—	3.3	27.5	—	Winton & Winton 1932
	4.3	23.8	57.4	15.6[5]	—	3.1	27.8	—	"
Pistacia sp.	7.0	8.1	42.6	24.8	21.6	2.9	21.1 [25.2[8]]	—	Kuzayli *et al.* 1966
Corylaceae									
Corylus colurna	4.1	14.3	62.8	15.2	5.2	2.4	28.1 [29.4[8]]	—	"
Corylus sp.	5.7	13.7	67.9	5.5	12.7	—	28.3 [29.7[8]]	—	Howes 1948
	5.8	13.4	66.2[1]	14.5[2]	3.2	2.7	26.9 [26.5[8]]	—	Watt & Merrill 1963
	7.1	18.7	67.4	11.2[5]	—	2.7	29.9	—	Winton & Winton 1932
(inc. shell)	3.7	16.2	67.8	13.5[5]	—	2.5	30.0	—	"

Table 7. Nutritional data - northern temperate nuts (cont.)

Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Fagaceae									
Castanea sativa	43.4	11.3	10.6	73.0	2.7	2.5	17.5 [18.6[8]]	—	Howes 1948
(dried)	6.1	11.4	8.3	74.7	3.1	2.6	17.0 [18.0[8]]	—	"
	55.6	5.0	5.4	82.0	4.7	2.9	16.0 [17.3[8]]	—	Kuzayli *et al.* 1966
	33.1	6.9	3.3	84.3[2]	2.4	3.1	15.9	0.2	Wainio & Forbes 1941
(fresh)	52.5	6.1	3.2[1]	86.3[2]	2.3	2.1	16.0 [17.1[8]]	—	Watt & Merrill 1963
(dried)	8.4	7.3	4.5[1]	83.1[2]	2.7	2.4	16.2 [17.2[8]]	—	"
(flour)	11.4	6.9	4.2[1]	83.7[2]	2.3	2.9	16.1 [17.0[8]]	—	"
	6.6	9.6	7.1	77.7	2.5	3.0	16.7	—	Winton & Winton 1932
	5.4	11.0	9.6	73.8	2.8	2.9	17.2	—	"
	52.2	6.5	3.4	84.7	2.9	2.3	15.9	—	"
	4.7	7.8	3.0	83.9	2.4	2.8	15.9	—	"
(flour)	14.0	9.3	4.1	81.3	3.3	2.9	16.1	—	"
Fagus sylvatica	5.0	30.5	49.6	7.6	7.3	4.9	24.7 [30.1[8]]	—	Drozdz 1968
	9.1	23.9	46.8	21.1	4.1	4.3	24.8	—	Winton & Winton 1932
("cake")	12.5	42.4	8.6	34.1	6.3	8.8	15.8	—	"
Juglandaceae									
Juglans regia	3.4	18.8	62.8	14.2	2.4	1.8	28.7 [30.1[8]]	—	Howes 1948
	1.2	14.9	61.3	17.6	3.7	2.4	28.0 [29.1[8]]	—	Kuzayli *et al.* 1966
	3.5	15.3	66.3[1]	14.2[2]	2.2	2.0	29.4 [28.2[8]]	—	Watt & Merrill 1963
	2.5	16.6	63.4	16.1	2.6	1.4	28.9	—	Winton & Winton 1932
Hippocastanaceae									
Aesculus hippocastanum	2.2	12.4	6.4	76.2	2.1	3.0	16.7	—	"
	2.6	9.1	6.5	78.5	2.4	2.8	16.5	—	"
(collected 1989)	3.4	7.6	10.6	79.4[6]	—	2.3	17.9 [16.7[9]]	—	10
(collected 1991, pieces, soaked)	60.7	9.3	7.1	81.5[6]	—	2.2	17.2 [16.8[9]]	—	10
(as previous, boiled and leached)	74.7	6.9	7.3	85.0[6]	—	0.8	17.5 [18.4[9]]	—	10

Table 7. Nutritional data - northern temperate nuts (cont.)

Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Pinaceae									
Pinus cembra	—	19.4	59.4	17.2	1.2	2.8	28.0	—	Winton & Winton 1932
P. pinea	6.2	36.1	51.4	6.9	1.5	4.1	26.2 [27.4[8]]	—	Howes 1948
	6.4	30.2	55.9	8.3	0.9	4.7	27.1 [27.7[8]]	—	Kuzayli *et al.* 1966
	5.6	32.9	50.2[1]	11.3[2]	1.0	4.6	26.0 [24.5[8]]	—	Watt & Merrill 1963
	6.1	33.9	47.9	6.4	—	—	24.5 [23.6[8]]	—	Winton & Winton 1932
	4.9	39.4	54.2	5.0[5]	—	1.2	27.6	—	"
Rosaceae									
Prunus dulcis	3.8	19.2	57.2	17.5	3.2	2.9	27.2 [28.2[8]]	—	Kuzayli *et al.* 1966
(dried)	4.7	19.5	56.9[1]	17.7[1]	2.7	3.1	27.2 [26.2[8]]	—	Watt & Merrill 1963
(sweet variety)	4.8	22.1	57.7	15.0	3.2	2.1	27.5	—	Winton & Winton 1932
(sweet variety)	6.0	25.0	56.4	15.3[5]	—	3.3	27.6	—	"
(sweet variety)	—	25.0	57.3	11.9	3.1	2.7	27.4	—	"
(almond butter)	0.9	22.8	62.1	8.2	3.9	2.9	28.2	—	"
(almond meal)	8.5	55.3	17.0	17.5	3.2	7.0	18.5	—	"
(almond paste)	24.2	17.3	31.5	38.8	10.3	2.1	20.9	—	"
4. SouthEast Asia, including Japan									
Fagaceae									
Castanea crenata	—	2.7	0.3	34.5	—	—	6.1 [6.5[8]]	—	Akazawa 1986b
	55.0	6.9	1.1	88.0	2.2	1.8	[16.7[8]]	—	Koyama 1978
Castanopsis cuspidata	—	3.2	0.8	57.7	—	—	10.1 [10.7[8]]	—	Akazawa 1986b
Hippocastanaceae									
Aesculus turbinata	—	5.3	4.5	73.7	—	—	14.4 [15.3[8]]	—	"
Juglandaceae									
Juglans sieboldiana	5.0	—	62.7	—	—	—	—	—	Winton & Winton 1932
Pterocarya rhoifolia	—	14.6	68.7	10.3	—	—	29.5 [28.2[8]]	—	Akazawa 1986b
Pinaceae									
Pinus densiflora	—	14.6	60.8	17.2	—	—	27.7 [26.5[8]]	—	"
P. koraiensis	—	14.8	78.9	3.7[5]	—	2.6	32.3	—	Winton & Winton 1932
Taxaceae									
Torreya nucifera	—	8.3	56.1	21.1	—	—	25.5 [25.5[8]]	—	Akazawa 1986b

Table 7. Nutritional data - northern temperate nuts (concluded)

1. Western North America									
Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Erythrobalanus									
Q. agrifolia	—	7.1	24.3[1]	13.2[3]	—	—	[13.2[8]]	20.3	Koenig & Heck 1988
(inc. shell)	29.1	6.9	18.4[1]	60.0	12.8	2.0	17.6	—	Wolf 1945
(inc. shell)	19.8	4.9	22.4[1]	58.0	12.8	1.9	18.4	—	"
Q. kelloggii	—	5.3	26.5	14.9[3]	—	—	[14.1[8]]	—	Koenig & Mumme 1987
(unleached flr.)	5.8	5.7	26.9[1]	63.3[2]	2.0	2.0	21.1	—	Merriam 1918
(leached flour)	11.3	5.1	22.3[1]	69.9[2]	2.3	0.3	20.3	—	"
	37.6	5.4	17.8[1]	52.4	22.6	1.7	15.9	2.9	Wagnon 1946 (cited in Duncan & Clawson 1980)
(inc. shell)	31.4	5.0	19.8[1]	60.9	12.5	1.8	17.9	—	Wolf 1945
Q. wislizenii	29.8	4.4	20.7[1]	57.5	16.0	1.4	17.6	6.6	Wagnon 1946 (cited in Duncan & Clawson 1980)
Lepidobalanus									
Q. douglasii	—	6.6	8.3	17.4[3]	—	—	[7.5[8]]	—	Koenig & Mumme 1987
	40.8	5.1	8.1[1]	73.3	12.0	1.7	15.6	6.1	Wagnon 1946 (cited in Duncan & Clawson 1980)
(inc. shell)	33.6	6.0	8.9[1]	72.0	10.8	2.3	15.8	—	Wolf 1945
Q. dumosa	44.6	4.2	6.1[1]	73.5	14.4	2.0	14.7	9.4	Wagnon 1946 (cited in Duncan & Clawson 1980)
Q. garryana (inc. shell)	30.7	4.3	4.9[1]	75.7	13.1	2.0	14.7	—	Wolf 1945
Q. lobata (flour)	8.7	6.2	20.4[1]	71.2[5]	—	2.2	20.0 [20.1[8]]	7.2	Chesnut 1974
(bread)	60.3	5.5	24.9[1]	68.0[5]	—	1.5	21.0 [23.3[8]]	trace	"
	—	5.5	5.6[1]	13.6[3]	—	—	[5.5[8]]	10.9	Koenig & Heck 1988
	40.6	4.7	7.2[1]	73.2	13.1	1.9	15.2	4.1	Wagnon 1946 (cited in Duncan & Clawson 1980)
(inc. shell)	40.8	5.4	6.1[1]	75.9	10.4	2.3	15.3	—	Wolf 1945
(Paso Robles, September 1990)	7.5	5.5	7.3	85.3[6]	—	1.9	17.3 [16.4[9]]	—	10
Protobalanus									
Q. chrysolepis	—	3.9	16.7[1]	12.6[3]	—	—	[11.4[8]]	9.1	Koenig & Heck 1988
(inc. shell)	42.1	4.5	9.5[1]	69.8	14.1	2.2	15.4	—	Wolf 1945
Quercus sp. (Southwest)	6.7	10.6[7]	5.8[1]	—	—	—	[17.1[8]]	—	Carpenter & Steggerda 1939
Lithocarpus densiflorus (inc. shell)	36.0	3.2	13.3[1]	59.8	22.1	1.6	15.0	—	Wolf 1945

Table 8. Nutritional data - acorns (continued over)

2. Eastern North America									
Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Erythrobalanus									
Q. coccinea (inc. shell)	—	4.2	14.6[1]	35.6[5]	—	—	11.8	—	Bonner 1971
(November)	—	7.8	30.8[1]	57.1	2.3	2.1	21.9	—	Korstian 1927
(previous sample, April)	—	7.5	23.1[1]	64.5	2.5	2.5	20.1	—	"
(different location)	—	—	—	—	—	—	—	6.7	"
Q. ellipsoidalis	5.0	—	21.1[1]	—	—	2.3	—	—	Lund & Sandstrom 1943
Q. falcata (inc. shell)	—	5.1	17.0[1]	23.0[5]	—	—	10.8	—	Bonner 1974
(var. *pagodaefolia*, inc. shell)	—	4.0	15.8[1]	29.5[5]	—	—	11.2	—	"
	21.8	—	—	—	—	—	[22.1[89]]	—	Burns & Viers 1973
(inc. shell)	10.6	4.2	15.6	57.7	20.6	1.9	15.7	—	King & McClure 1944
(inc. shell)	19.8	7.0	22.7[1]	48.6	19.9	1.8	17.4	—	Short 1976
Q. ilicifolia (inc. shell)	9.6	6.1	19.4	54.6	18.3	1.7	17.0	—	King & McClure 1944
	42.0	10.3	20.0	64.6	3.0	2.1	19.5	11.3	Wainio & Forbes 1941
	3.5	10.8	16.5	67.5	3.5	1.8	18.7	—	Wright 1941
Q. incana (inc. shell)	15.7	5.9	12.7	67.1	12.5	1.8	16.4	—	King & McClure 1944
(inc. shell)	17.4	6.9	26.2[1]	49.0	15.8	2.1	18.7	—	Short 1976
Q. laurifolia	51.3	—	—	—	—	—	[20.3[89]]	—	Burns & Viers 1973
Q. marilandica	40.7	—	—	—	—	—	[22.6[89]]	—	"
(inc. shell)	14.7	6.3	10.7	60.1	20.9	2.0	14.6	—	King & McClure 1944
(inc. shell)	7.8	5.5	18.2	52.6	21.8	2.0	16.1	—	"
(inc. shell)	8.2	5.8	17.7	53.0	21.8	1.8	16.0	—	"

Table 8. Nutritional data - acorns (cont.)

Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Q. nigra									
(poorly developed)	8.4	4.0	19.9[1]	59.8	14.5	1.9	17.6	—	Billingsley & Arner 1970
(inc. shell)	—	3.8	20.3[1]	25.8[5]	—	—	12.3	—	Bonner 1971
	24.8	—	—	—	—	—	[21.3[89]]	—	Burns & Viers 1973
(inc. shell)	7.1	4.3	22.8	54.2	17.6	1.2	17.8	—	King & McClure 1944
(inc. shell)	7.7	4.0	21.8	54.2	18.9	1.2	17.4	—	"
(inc. shell)	7.5	3.7	20.9	54.8	19.0	1.7	17.1	—	"
(previous sample, germinated)	5.1	4.6	23.7	50.5	19.6	1.6	17.6	—	"
	—	3.8	14.6[1]	48.7	17.2	1.6	13.8	—	Landers *et al.* 1977
(inc. shell)	18.1	4.9	21.1[1]	54.0	17.6	2.4	17.3	—	Short 1976
Q. nuttallii									
(inc. shell)	—	4.5	13.2[1]	46.2[5]	—	—	13.0	—	Bonner 1974
	52.6	—	—	—	—	—	[18.1[89]]	—	Burns & Viers 1973
(inc. shell)	5.7	3.8	15.0	66.7	13.2	1.4	16.9	—	King & McClure 1944
Q. palustris									
(inc. shell)	—	3.8	15.4[1]	45.4[5]	—	—	13.6	—	Bonner 1974
	—	5.9	26.1	—	—	—	—	—	Earle & Jones 1962 (cited in Asch *et al.*1972)
	32.7	7.2	22.0	64.7	3.9	2.1	19.7 [17.4[8]]	—	Gaussen & Rouquette 1949
(inc. shell)	8.8	7.2	17.8	58.4	15.6	1.3	17.2	—	King & McClure 1944
	—	—	—	—	—	—	[21.1[8]]	—	Robel *et al.* 1979
	—	—	—	—	—	—	[21.2[8]]	—	"
Q. phellos									
(inc. shell)	—	5.9	19.6[1]	31.2[5]	—	—	13.3	—	Bonner 1971
	45.1	—	—	—	—	—	[22.2[89]]	—	Burns & Viers 1973
(inc. shell)	11.1	4.2	19.6	54.7	19.4	2.1	16.7	—	King & McClure 1944
(inc. shell)	13.4	5.1	18.5	55.9	18.8	1.7	16.7	—	"
(inc. shell)	9.3	4.6	23.0	52.8	18.3	1.4	17.7	—	"
(inc. shell)	11.3	4.9	21.9	52.8	18.6	1.8	17.4	—	"
(previous sample, shell only)	7.6	2.5	0.5	41.1	54.6	1.4	7.2	—	"
(previous sample, kernel only)	5.6	5.8	29.5	60.4	2.5	1.7	21.6	—	"
(inc. shell)	20.5	5.5	20.0[1]	53.5	18.9	2.1	16.9	—	Short 1976

Table 8. Nutritional data - acorns (cont.)

Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Q. rubra	14.9	6.9	18.9	68.3	2.8	3.2	19.1	—	Baumgras 1944
	36.9	5.2	14.7	59.9	17.9	—	15.9 [13.4[8]]	—	Forbes *et al.* 1941
	22.5	6.4	21.0	68.0	2.4	2.2	19.7 [17.7[8]]	—	Gaussen & Rouquette 1949
	—	4.7-5.9	16.2-22.5	65.9-72.2	3.0-5.4	2.4-2.9	—	—	Gysel 1957
	—	—	—	—	—	—	[20.6[89]]	—	Havera & Smith 1979
(November)	—	7.2	22.5[1]	65.4	2.4	2.7	20.0	7.4	Korstian 1927
(previous sample, April)	—	6.9	20.1[1]	67.3	2.8	2.9	19.4	—	"
	—	—	—	—	—	—	[20.4[89]]	—	Lewis 1982
	5.2	5.9	21.7[1]	68.7[6]	—	3.7	20.0	—	Lund & Sandstrom 1943
	4.5	—	12.1[1]	—	—	3.5	—	—	"
	36.7	3.4	8.6[1]	55.4	28.7	—	12.6 [20.9[8]]	—	Pekins & Mautz 1988
	—	—	—	—	—	—	[21.8[8]]	—	Robel *et al.* 1979
	—	6.3	23.0[1]	—	—	—	[17.2[8]]	13.0	Servello & Kirkpatrick 1989
(inc. shell)	20.6	4.9	14.0[1]	52.3	26.4	2.4	14.4	—	Short 1976
(inc. shell)	10.3	5.8	19.7[1]	51.8	20.3	2.5	16.6	—	Torgerson & Pfander 1971
	38.2	6.6	20.8	67.1	3.1	2.4	19.6	9.8	Wainio & Forbes 1941
	1.8	7.7	23.0	62.1	4.9	2.2	19.8	—	Wright 1941
Q. shumardii (inc. shell)	—	3.8	9.8[1]	29.3[5]	—	—	9.0	—	Bonner 1971
	45.5	—	—	—	—	—	[21.3[89]]	—	Burns & Viers 1973
	—	—	20.3[1]	—	—	—	[21.8[8]]	—	Smith & Follmer 1972
Q. velutina	9.0	6.9	23.0	65.2	3.0	3.3	20.1	—	Baumgras 1944
	38.5	—	—	—	—	—	[19.7[89]]	—	Burns & Viers 1973
("medium site")	—	6.8-7.1	23.1-25.1	62.8-66.5	2.7-3.4	1.6-1.8	—	—	Gysel 1957
("poor site")	—	5.9-7.0	21.0-24.5	64.2-68.0	3.0-3.2	1.7-1.8	—	—	"
	—	—	—	—	—	—	[22.4[89]]	—	Havera & Smith 1979
(inc. shell)	12.8	5.7	17.5[1]	57.9	16.6	2.3	—	—	Short 1976

Table 8. Nutritional data - acorns (cont.)

Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Lepidobalanus									
Q. alba	24.3	7.8	5.8	81.2	4.1	1.1	16.5	—	Baumgras 1944
(inc. shell)	—	4.6	2.9[1]	46.6[5]	—	—	9.3	—	Bonner 1971
	53.8	—	—	—	—	—	[16.3[89]]	—	Burns & Viers 1973
("good site")	—	6.5	4.8	83.3	2.7	2.7	16.2	—	Gysel 1957
("medium site")	—	6.4-7.7	6.0-6.9	81.5-82.2	2.2-3.2	2.0-2.3	—	—	"
	—	—	—	—	—	—	[18.7[89]]	—	Havera & Smith 1979
	39.7	6.3	6.8	82.6	1.8	2.6	16.8 [10.5[8]]	4.4	Henry 1950 (cited in Hilliard 1980)
(inc. shell)	9.7	6.7	5.7	67.3	17.4	3.2	14.0	—	King & McClure 1944
(November)	—	7.4	6.8[1]	81.4	1.8	2.6	16.8	4.4	Korstian 1927
(previous sample, April)	—	7.8	2.6[1]	84.6	2.5	2.4	15.8	—	"
(different location)	—	—	—	—	—	—	—	7.8	"
	—	—	—	—	—	—	[17.8[89]]	—	Lewis 1982
	3.1	8.7	8.2[1]	80.4[6]	—	2.8	17.4	—	Lund & Sandstrom 1943
	—	7.3	8.3[1]	—	—	—	[15.9[8]]	3.3	Servello & Kirkpatrick 1989
(inc. shell)	39.5	4.6	5.8[1]	68.3	18.6	2.7	13.9	—	Short 1976
	—	—	4.6[1]	—	—	—	[17.4[8]]	—	Smith & Follmer 1972
	47.3	6.3	6.3[1]	82.3	2.5	2.6	16.6	5.6	Wainio & Forbes 1941
Q. durandii (inc. shell)	—	6.2	3.8[1]	44.9[5]	—	—	9.6	—	Bonner 1971
Q. havardii (inc. shell)	9.0	7.7	6.7	71.4	12.2	2.3	15.2	—	King & McClure 1944
Q. lyrata (inc. shell)	—	4.6	0.9[1]	49.8[5]	—	—	9.1	—	Bonner 1974
	48.6	—	—	—	—	—	[17.1[89]]	—	Burns & Viers 1973
Q. macrocarpa (inc. shell)	—	4.3	4.8[1]	45.9[5]	—	—	9.9	—	Bonner 1974
	—	—	—	—	—	—	[17.8[89]]	—	Burns & Viers 1973
	—	—	—	—	—	—	[21.1[89]]	—	Havera & Smith 1979
	5.8	8.5	8.4[1]	80.0	—	3.1	17.4	—	Lund & Sandstrom 1943
	—	—	9.8[1]	—	—	—	[18.5[8]]	—	Smith & Follmer 1972

Table 8. Nutritional data - acorns (cont.)

Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Q. michauxii (inc. shell)	—	4.1	3.3[1]	56.1[5]	—	—	10.9	—	Bonner 1974
(inc. shell)	6.9	6.4	3.3	72.9	15.2	2.2	14.0	—	King & McClure 1944
(inc. shell)	7.4	3.6	14.0	60.4	20.3	1.8	15.5	—	"
(inc. shell)	45.5	4.4	2.9[1]	67.6	22.3	2.8	12.6	—	Short 1976
Q. muehlenbergii (inc. shell)	—	4.4	6.6[1]	34.5[5]	—	—	8.7	—	Bonner 1971
Q. prinoides	44.2	7.6	6.3	81.7	2.4	2.0	16.7	4.4	Wainio & Forbes 1941
Q. prinus	42.9	—	—	—	—	—	[17.0[89]]	—	Burns & Viers 1973
(November)	—	8.5	4.6[1]	82.2	2.5	2.3	16.3	7.8	Korstian 1927
(previous sample, April)	—	8.9	1.9[1]	83.2	3.1	3.0	15.5	—	"
(different location)	—	—	—	—	—	—	—	8.9	"
	—	—	—	—	—	—	[18.1[89]]	—	Lewis 1982
	—	5.9	8.8[1]	—	—	—	[13.8[8]]	8.1	Servello & Kirkpatrick 1989
	34.9	—	—	—	—	1.1	—	8.8	Trimble 1896
	—	6.9	5.1	83.2	2.6	2.2	16.4	10.4	Wainio & Forbes 1941
Q. stellata (inc. shell)	—	3.8	5.2[1]	37.9[5]	—	—	8.6	—	Bonner 1971
	39.5	—	—	—	—	—	[18.3[89]]	—	Burns & Viers 1973
(inc. shell)	7.7	5.2	5.7	66.7	19.5	3.0	13.7	—	King & McClure 1944
(inc. shell)	8.2	4.8	7.6	65.2	19.6	2.8	14.1	—	"
	—	6.3	10.7[1]	60.1	20.9	2.0	14.6	—	Landers *et al.* 1979
(inc. shell)	32.7	6.8	6.7[1]	65.3	18.1	3.1	14.1	—	Short 1976
Q. virginiana	29.0	7.9	2.5[1]	62.0	23.2	4.9	12.2	—	Beck & Beck 1955
(inc. shell)	—	4.4	8.2[1]	46.4[5]	—	—	11.2	—	Bonner 1971
	68.2	—	—	—	—	—	[17.3[89]]	—	Burns & Viers 1973
(inc. shell)	10.2	5.2	8.6	68.0	16.7	1.7	14.9	—	King & McClure 1944
(inc. shell)	28.7	5.8	6.1[1]	71.7	14.6	1.8	14.7	—	Short 1976
Quercus sp.	55.3	5.6	4.3[1]	77.9[2]	—	2.3	15.0	—	Smith 1929

Table 8. Nutritional data - acorns (cont.)

3. Europe, the Mediterranean and Southwest Asia									
Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extrct	Fibre				
Cerris									
Q. brantii									
(Turkey, October 1990)	1.0	3.8	7.5	86.4[6]	—	1.9	17.3 [17.5[9]]	—	10
(Turkey, October 1990)	9.1	3.8	6.3	88.7[6]	—	1.2	17.2 [16.8[9]]	—	10
(Turkey, October 1990)	5.0	3.7	3.7	91.4[6]	—	1.3	16.6 [16.3[9]]	—	10
(Turkey, October 1990)	2.0	4.2	8.4	86.1[6]	—	1.4	17.6 [17.2[9]]	—	10
(Turkey, October 1990)	2.8	2.1	5.1	91.9[6]	—	0.9	16.9 [16.1[9]]	—	10
(Turkey, October 1990)	3.0	1.6	4.9	92.4[6]	—	1.0	16.9 [16.8[9]]	—	10
Q. cerris									
(inc. shell)	—	—	—	—	—	—	[18.9]	—	Papp 1985a
	43.9	6.3	4.2	82.3	4.5	2.6	15.8	—	Petrucci 1947
(inc. shell)	39.5	5.7	4.0	77.2	10.1	3.0	14.8	—	"
(inc. shell)	42.4	6.3	3.5	76.2	11.2	2.8	14.6	—	"
Q. ithaburensis ssp. *macrolepis*	—	—	—	—	—	—	—	16	Irgens-Moller 1955
(Greece, August 1989)	6.1	4.4	6.0	88.1[6]	—	1.6	17.1 [15.9[9]]	—	10
Q. suber	34.7	6.2	5.8	82.4	4.6	1.8	16.4 [14.6[8]]	—	Gaussen & Rouquette 1949
Ilex									
Q. coccifera	34.3	3.7	5.2	86.6	2.5	2.1	16.4 [14.1[8]]	—	Gaussen & Rouquette 1949
(Turkey, October 1990)	12.3	2.4	3.9	92.5[6]	—	1.2	16.7 [16.9[9]]	—	10

Table 8. Nutritional data - acorns (cont.)

Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Q. ilex									
	33.1	4.2	8.2	82.5	3.3	1.9	16.9 [14.8[8]]	—	Gaussen & Rouquette 1949
	26.9	5.9	10.7	78.1	1.6	2.7	17.5	0.4	Mazuelos Vela *et al.* 1967
	32.3	5.7	9.2	81.2	1.4	2.1	17.4	0.5	"
	26.6	5.8	7.5	82.1	1.4	2.8	16.9	0.4	"
	30.6	5.9	10.9	78.5	1.6	2.8	17.6	0.4	"
	30.0	5.0	10.2	79.1	1.5	3.6	17.3	0.4	"
	29.6	5.9	10.4	78.0	2.1	3.0	17.3	0.4	"
	26.6	5.4	9.4	80.2	1.6	2.9	17.2	0.5	"
	29.7	5.4	10.6	79.7	2.0	2.0	17.6	0.4	"
	40.5	4.4	5.1	84.4	3.7	2.5	16.1	—	Petrucci 1947
(inc. shell)	40.4	3.9	4.9	78.3	10.7	2.2	15.0	—	"
(inc. shell)	40.3	4.2	4.4	79.2	9.8	2.5	15.0	—	"
(Andalucia, July 1991)	0.6	6.3	7.9	83.9[6]	—	1.9	17.4 [16.4[9]]	—	10
Quercus									
Q. infectoria ssp. *boissieri*									
(Turkey, Oct. 1990)	3.1	2.6	1.8	94.3[6]	—	1.3	16.2 [16.1[9]]	—	10
(Turkey, Oct. 1990)	2.8	3.1	1.6	93.8[6]	—	1.5	16.1 [15.9[9]]	—	10
Q. petraea									
	14.2	5.7	6.9	80.4	4.5	2.5	16.4 [17.6[8]]	—	Drozdz 1968
	41.2	6.2	4.4	84.9	2.3	2.3	16.3 [13.8[8]]	—	Gaussen & Rouquette 1949
	40.2	8.5	5.4	79.4	3.7	3.0	16.1	—	Petrucci 1947
(inc. shell)	44.8	7.9	4.2	74.2	10.2	3.5	14.8	—	"
(inc. shell)	38.0	7.9	4.6	72.6	12.0	2.9	14.7	—	"
Q. pubescens	33.1	4.9	4.7	85.7	2.5	2.2	16.3 [14.6[8]]	—	Gaussen & Rouquette 1949
Q. pyrenaica	40.6	6.7	4.9	83.9	2.4	2.1	16.4 [14.6[8]]	—	"

Table 8. Nutritional data - acorns (cont.)

Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Q. robur	35.8	5.6	5.2	84.1	2.8	2.3	16.3 [14.6[8]]	—	Gaussen & Rouquette 1949
(inc. shell)	—	—	—	—	—	—	[19.5]	—	Papp 1985a
	35.0	5.4	5.8	83.9	2.4	2.4	16.5	—	Petrucci 1947
(inc. shell)	33.1	5.0	4.9	77.3	10.3	2.5	15.0	—	"
(inc. shell)	33.5	5.0	4.9	74.5	13.1	2.5	14.6	—	"
(Hertfordshire, September 1989)	1.0	8.5	4.2	85.1[6]	—	2.2	16.6 [16.2[9]]	—	10
(as previous, different tree)	1.4	7.8	5.1	85.0[6]	—	2.1	16.8 [14.6[9]]	—	10
(Sussex, October 1989)	1.1	5.6	2.4	89.5[6]	—	2.5	16.2 [15.9[9]]	—	10
(London, October 1989)	0.8	6.6	4.2	87.3[6]	—	1.9	16.6 [16.1[9]]	—	10
(Bucks., October 1989)	3.2	7.8	5.2	85.0[6]	—	2.0	16.9 [15.7[9]]	—	10
(Surrey, August 1989)	10.5	7.8	3.2	86.7[6]	—	2.3	16.4 [15.7[9]]	—	10
(same tree, October 1989)	0.9	5.9	3.7	88.2[6]	—	2.2	16.5 [16.1[9]]	—	10
(Kent, October 1989)	0.1	7.3	3.1	87.7[6]	—	1.9	16.4 [16.3[9]]	—	10
(same tree, October 1991)	61.4	5.8	3.2	89.0[6]	—	2.1	16.4 [15.3[9]]	—	10
(as previous, roasted)	24.0	7.0	5.4	85.3[6]	—	2.3	16.8 [16.0[9]]	—	10
(Kent, Oct 1989, several trees, flour)	6.3	6.9	5.0	85.3[6]	—	2.7	16.7 [15.8[9]]	—	10
(as previous, partly leached)	8.3	7.4	5.0	86.7[6]	—	0.9	17.0 [16.0[9]]	—	10
(as previous, bread with clay)	6.0	6.8	2.6	83.6[6]	—	7.1	15.5 [15.4[9]]	—	10
(as previous, bread without clay)	5.5	7.5	1.5	89.4[6]	—	1.6	16.1 [15.9[9]]	—	10
Q. robur/petraea	29.8	7.7	4.4	68.4[4]	16.8	2.7	13.9	—	Braude 1943
(shells)	14.8	2.9	1.1	58.5[4]	36.2	1.4	10.3	—	"
(inc. shell)	27.0	6.7	3.7	66.2[4]	21.0	2.5	13.1	—	"
	13.9	9.2	5.3	78.7	4.2	2.6	16.1	—	Winton & Winton 1932
	3.3	7.8	4.9	82.2	2.4	2.8	16.3	—	"
	1.5	6.8	5.1	83.8	2.2	2.3	16.5	—	"
Quercus sp. (Lebanon)	39.1	1.5	2.0	94.1	1.0	1.5	16.0 [16.9[8]]	—	Kuzayli *et al.* 1966

Table 8. Nutritional data - acorns (cont.)

4. East and Southeast Asia, including Japan									
Species	Water	Crude Protein	Fats	Carbohydrates		Ash	Energy Value (kJ/g)	Tannins	Source
				N-free Extract	Fibre				
Cyclobalanopsis									
Q. acuta	—	—	—	—	—	—	—	1.2	Matsuyama 1981
Q. glauca	12.6	3.8	5.7	68.1[2]	2.2	1.5	13.7	—	Gul & Khan 1982
Q. leucotrichophora	12.2	3.4	18.2[1]	70.4[2]	1.6	1.6	18.6	4.8	Puntambekar & Varma 1934
Q. myrsinaefolia	—	—	—	—	—	—	—	2.5	Matsuyama 1981
Quercus									
Q. acutissima	—	—	—	—	—	—	—	3.4	"
(in US, inc. shell)	33.1	6.6	4.7[1]	73.2	12.4	3.1	14.6	—	Short 1976
Q. dealbata (small acorns)	—	9.5	23.7[1]	59.9[2]	—	6.8	20.0 [23.7[8]]	—	Tripathi & Khan 1990
(medium acorns)	—	9.0	39.6[1]	45.6[2]	—	5.7	23.5 [24.4[8]]	—	"
(large acorns)	—	8.6	39.0[1]	46.4[2]	—	5.9	23.3 [24.8[8]]	—	"
Q. dentata	—	—	—	—	—	—	—	4.0	Matsuyama 1981
Q. dilatata	1.4	4.3	14.4	63.1[2]	1.5	1.9	16.2	—	Gul & Khan 1982
Q. griffithii (small acorns)	—	9.7	32.7[1]	55.2[2]	—	2.3	22.6 [24.0[8]]	—	Tripathi & Khan 1990
(medium acorns)	—	10.2	37.9[1]	48.4[2]	—	3.5	23.5 [24.6[8]]	—	"
(large acorns)	—	8.3	39.1[1]	48.9[2]	—	3.8	23.7 [24.2[8]]	—	"
Q. ilex	11.3	4.5	16.3	67.8[2]	2.1	2.4	17.6	—	Gul & Khan 1982
Q. mongolica	—	—	—	—	—	—	—	6.4	Matsuyama 1981
Q. serrata	—	—	—	—	—	—	—	6.7	"
Quercus sp. (flour, Korea)	0.2	1.8	2.4	95.1[6]	—	0.8	16.4 [15.4[9]]	—	10

Table 8. Nutritional data - acorns (concluded)

Samples analysed	Taxonomic Group		Crude Protein	Fats	Carbohydrates		Ash
					N-FE	Fibre	
1. Western North America							
All samples	*Erythrobalanus*	Mean Range	**5.3** 4.4-6.9	**19.8** 17.8-22.4	**57.8** 52.4-60.9	**15.3** 12.5-22.6	**1.8** 1.4-2.0
	Lepidobalanus	Mean Range	**5.0** 4.2-6.0	**6.9** 4.9-8.9	**75.6** 72.0-85.3	**12.3** 10.4-14.4	**2.0** 1.7-2.3
	Combined	Mean Range	**5.2** 4.2-6.9	**12.3** 4.9-22.4	**68.1** 52.4-85.3	**13.7** 10.4-22.6	**1.9** 1.4-2.3
Samples without shells	*Erythrobalanus*	Mean Range	**4.9** 4.4-5.4	**19.3** 17.8-20.7	**55.0** 52.4-57.5	**19.3** 16.0-22.6	**1.6** 1.4-1.7
	Lepidobalanus	Mean Range	**4.9** 4.2-5.5	**7.2** 6.1-8.1	**76.3** 73.2-85.3	**13.2** 12.0-14.4	**1.9** 1.7-2.0
	Combined	Mean Range	**4.9** 4.2-5.5	**11.2** 6.1-20.7	**69.2** 52.4-85.3	**15.6** 12.0-22.6	**1.8** 1.4-2.0
Samples with shells	*Erythrobalanus*	Mean Range	**5.6** 4.9-6.9	**20.2** 18.4-22.4	**59.6** 58.0-60.9	**12.7** 12.5-12.8	**1.9** 1.8-2.0
	Lepidobalanus	Mean Range	**5.2** 4.3-6.0	**6.6** 4.9-8.9	**74.5** 72.0-75.9	**11.4** 10.4-13.1	**2.2** 2.0-2.3
	Combined	Mean Range	**5.4** 4.3-6.9	**13.4** 4.9-22.4	**67.1** 58.0-75.9	**12.1** 10.4-13.1	**2.1** 1.8-2.3
2. Eastern North America							
All samples	*Erythrobalanus*	Mean Range	**6.0** 3.4-10.8	**19.8** 8.6-30.8	**59.0** 48.6-68.7	**13.4** 2.3-28.7	**2.1** 1.2-3.7
	Lepidobalanus	Mean Range	**6.7** 3.6-8.9	**6.2** 1.9-14.0	**74.1** 60.1-84.6	**11.5** 1.8-23.2	**2.5** 1.1-4.9
	Combined	Mean Range	**6.2** 3.4-10.8	**14.5** 1.9-30.8	**64.9** 48.6-84.6	**12.7** 1.8-28.7	**2.3** 1.1-4.9
Samples without shells	*Erythrobalanus*	Mean Range	**6.9** 3.4-10.8	**20.9** 8.6-30.8	**63.9** 55.4-68.7	**6.3** 2.3-28.7	**2.5** 1.7-3.7
	Lepidobalanus	Mean Range	**7.5** 6.3-8.9	**5.8** 1.9-10.7	**79.2** 60.1-84.6	**5.8** 1.8-23.2	**2.6** 1.1-4.9
	Combined	Mean Range	**7.2** 3.4-10.8	**14.1** 1.9-30.8	**70.8** 55.4-84.6	**6.1** 1.8-28.7	**2.5** 1.1-4.9
Samples with shells	*Erythrobalanus*	Mean Range	**5.3** 3.7-7.2	**18.9** 10.7-26.2	**55.3** 48.6-67.1	**18.7** 12.5-26.4	**1.8** 1.2-2.5
	Lepidobalanus	Mean Range	**5.6** 3.6-7.7	**6.6** 2.9-14.0	**67.7** 60.4-72.9	**17.7** 12.2-22.3	**2.5** 1.7-3.2
	Combined	Mean Range	**5.4** 3.6-7.7	**14.8** 2.9-26.2	**59.4** 48.6-72.9	**18.3** 12.2-26.4	**2.1** 1.2-3.2

Table 9. Regional and taxonomic summary - major nutrients in acorns (continued over)

3. Europe, the Mediterranean and Southwest Asia							
Samples analysed	Taxonomic Group		Crude Protein	Fats	Carbohydrates		Ash
					N-FE	Fibre	
All samples	*Cerris*	Mean Range	**4.4** 1.6-6.3	**5.4** 3.5-8.4	**85.7** 76.2-92.4	**7.6** 4.5-11.2	**1.8** 0.9-3.0
	Ilex	Mean Range	**4.9** 2.4-6.3	**7.9** 3.9-10.9	**81.6** 78.0-92.5	**3.3** 1.4-10.7	**2.4** 1.2-3.6
	Quercus	Mean Range	**6.5** 2.6-9.2	**4.3** 1.6-6.9	**82.7** 66.2-94.3	**7.1** 2.2-21.0	**2.3** 1.3-3.5
	Total	Mean Range	**5.5** 1.5-9.2	**5.5** 1.6-10.9	**83.2** 66.2-94.3	**5.5** 1.0-21.0	**2.2** 0.9-3.6
Samples without shells	*Cerris*	Mean Range	**4.0** 1.6-6.3	**5.8** 3.7-8.4	**87.7** 82.3-92.4	**4.6** 4.5-4.6	**1.5** 0.9-2.6
	Ilex	Mean Range	**5.1** 2.4-6.3	**8.4** 3.9-10.9	**82.1** 78.0-92.5	**2.1** 1.4-3.7	**2.4** 1.2-3.6
	Quercus	Mean Range	**6.5** 2.6-9.2	**4.3** 1.6-6.9	**84.9** 68.4-94.3	**4.2** 2.2-16.8	**2.2** 1.3-3.0
	Total	Mean Range	**5.5** 1.5-9.2	**5.7** 1.6-10.9	**84.8** 68.4-94.3	**3.2** 1.0-16.8	**2.1** 0.9-3.6
Samples with shells	*Cerris*	Mean Range	**6.0** 5.7-6.3	**3.8** 3.5-4.0	**76.7** 76.2-77.2	**10.7** 10.1-11.2	**2.9** 2.8-3.0
	Ilex	Mean Range	**4.1** 3.9-4.2	**4.7** 4.4-4.9	**78.8** 78.3-79.2	**10.3** 9.8-10.7	**2.4** 2.2-2.5
	Quercus	Mean Range	**6.5** 5.0-7.9	**4.5** 3.7-4.9	**73.0** 66.2-77.3	**13.3** 10.2-21.0	**2.8** 2.5-3.5
	Total	Mean Range	**5.8** 3.9-7.9	**4.3** 3.5-4.9	**75.1** 66.2-79.2	**12.0** 9.8-21.0	**2.7** 2.2-3.5

Table 9. Regional and taxonomic summary - major nutrients in acorns (concluded)

1. Western North America		
Taxonomic Group		Tannins (%)
Erythrobalanus	Mean Range	**9.9** 2.9-20.3
Lepidobalanus	Mean Range	**7.6** 4.1-10.9
Total	Mean Range	**8.7** 2.9-20.3
2. Eastern North America		
Erythrobalanus	Mean Range	**9.6** 6.7-13.0
Lepidobalanus	Mean Range	**6.7** 3.3-10.4
Total	Mean Range	**7.6** 3.3-13.0
3. Eastern and Western North America Combined		
Erythrobalanus	Mean Range	**9.8** 2.9-20.3
Lepidobalanus	Mean Range	**7.0** 3.3-10.9
Total	Mean Range	**8.0** 2.9-20.3
4. East and Southeast Asia, including Japan		
Cyclobalanopsis	Mean Range	**2.8** 1.2-4.8
Quercus	Mean Range	**5.1** 3.4-6.7
Total	Mean Range	**4.1** 1.2-6.7

Table 10. Regional and taxonomic summary - tannins in acorns

Samples analysed	Taxonomic Group		Fibre (%)	Energy Value (kJ/g) (Calculated)	Energy Value (kJ/g) (Measured)
		1. Western North America			
All samples	*Erythrobalanus*	Mean Range	**15.3** 12.5-22.6	**17.5** 15.9-18.4	**13.7** 13.2-14.1
	Lepidobalanus	Mean Range	**12.3** 10.4-14.4	**15.5** 14.7-17.3	**9.8** 5.5-16.4
	Total	Mean Range	**14.4** 10.4-22.6	**16.2** 14.7-18.4	**12.2** 5.5-17.1
Samples without shells	*Erythrobalanus*	Mean Range	**19.3** 16.0-22.6	**16.8** 15.9-17.6	**13.7** 13.2-14.1
	Lepidobalanus	Mean Range	**13.2** 12.0-14.4	**15.7** 14.7-17.3	**9.8** 5.5-16.4
	Total	Mean Range	**15.6** 12.0-22.6	**16.1** 14.7-17.6	**12.2** 5.5-17.1
Samples with shells	*Erythrobalanus*	Mean Range	**12.7** 12.5-12.8	**18.0** 17.6-18.4	**0.0** 0.0
	Lepidobalanus	Mean Range	**11.4** 10.4-13.1	**15.3** 14.7-15.8	**0.0** 0.0 0.0
	Total	Mean Range	**13.6** 10.4-22.1	**16.3** 14.7-18.4	**0.0** 0.0
		2. Eastern North America			
All samples	*Erythrobalanus*	Mean Range	**13.4** 2.3-28.7	**17.8** 12.6-21.9	**20.2** 13.4-22.6
	Lepidobalanus	Mean Range	**11.5** 1.8-23.2	**15.3** 12.2-17.4	**17.0** 10.5-21.1
	Total	Mean Range	**12.7** 1.8-28.7	**16.8** 12.2-21.9	**18.8** 10.5-22.6
Samples without shells	*Erythrobalanus*	Mean Range	**6.3** 2.3-28.7	**19.1** 12.6-21.9	**20.2** 13.4-22.6
	Lepidobalanus	Mean Range	**5.8** 1.8-23.2	**16.1** 12.2-17.4	**17.0** 10.5-21.1
	Total	Mean Range	**6.1** 1.8-28.7	**17.8** 12.2-21.9	**18.8** 10.5-22.6
Samples with shells	*Erythrobalanus*	Mean Range	**18.8** 12.5-26.4	**16.8** 14.4-18.7	**0.0** 0.0
	Lepidobalanus	Mean Range	**17.7** 12.2-22.3	**14.2** 12.6-15.5	— —
	Total	Mean Range	**18.4** 12.2-26.4	**15.9** 12.6-18.7	— —

Table 11. Regional and taxonomic summary - energy value of acorns (continued over)

3. Europe, the Mediterranean and Southwest Asia					
Samples analysed	Taxonomic Group		Fibre	Energy Value (kJ/g) (Calculated)	Energy Value (kJ/g) (Measured)
All samples	*Cerris*	Mean Range	**7.6** 4.5-11.2	**16.5** 14.6-17.6	**16.7** 14.6-18.9
	Ilex	Mean Range	**3.3** 1.4-10.7	**16.8** 15.0-17.6	**15.3** 14.1-16.9
	Quercus	Mean Range	**7.1** 2.2-21.0	**15.9** 13.1-16.9	**16.0** 13.8-19.5
	Total	Mean Range	**5.5** 1.0-21.0	**16.3** 13.1-17.6	**16.2** 13.8-19.5
Samples without shells	*Cerris*	Mean Range	**4.6** 4.5-4.6	**16.9** 15.8-17.6	**16.4** 14.6-17.5
	Ilex	Mean Range	**2.1** 1.4-3.7	**17.1** 16.1-17.6	**15.3** 14.1-16.9
	Quercus	Mean Range	**4.2** 2.2-16.8	**16.3** 13.9-16.9	**15.7** 13.8-17.6
	Total	Mean Range	**3.2** 1.0-16.8	**16.6** 13.9-17.6	**15.9**-17.6 13.8
Samples with shells	*Cerris*	Mean Range	**10.7** 10.1-11.2	**14.7** 14.6-14.8	**18.9** 18.9-18.9
	Ilex	Mean Range	**10.3** 9.8-10.7	**15.0** 15.0-15.0	— —
	Quercus	Mean Range	**13.3** 10.2-21.0	**14.4** 13.1-15.0	**19.5** 19.5-19.5
	Total	Mean Range	**10.9** 1.0-21.0	**14.8** 13.1-16.0	**18.4** 16.9-19.5

Table 11. Regional and taxonomic summary - energy value of acorns (concluded)

APPENDIX 2. TANNINS

2.1. INTRODUCTION

Though the presence of polyphenolics in some plants has been shown to correlate with dormancy (e.g., Khan 1977; Werker *et al.* 1979), Korstian (1927) dismissed relative tannin levels as explanations for delay in germination of the red oaks, since he found these to be virtually the same in acorns of red and white oak groups. Most other studies of tannins in acorns suggest that red oaks do possess greater quantities of tannins (see 6.3.).

One prime role of tannins in plant tissues of many kinds is thought to be that of predator deterrence, and Harborne (1982) comments that they are probably the most important herbivore barrier in angiosperms. Bradbeer (1988) suggests that tannins in seeds may also be important in protecting against micro-organisms, and that they may have allelopathic affects against other seeds or roots. The way in which tannins achieve any anti-predatory effect however, and especially any supposed co-evolutionary role in relation to this function (see, e.g., Janzen 1969, 1971) seems to have become more uncertain the more tannins have been studied (Bradbeer 1988; Haslam 1989).

The astringent taste present in acorns seems to be stronger at the apical end of acorns, and squirrels have been reported to reject this part in germinating acorns (Smith and Follmer 1972), though this was thought to correlate with the development of cellulose- and lignin-rich structural and vascular tissue associated with the germination process. *Curculio* larvae (see Appendix 4, 4.2.2., 4.2.6.) seem to concentrate their activity in the lower part of the acorn and comments (by foresters) that those acorns which have not had the cotyledons nearest to the developing radicle and plumule eaten will germinate suggest that this may be a common (and perhaps evolutionarily significant) feature.

2.2. DEFINITIONS AND TYPES OF TANNINS

One complication with any study of tannins is the vast variety of compounds which are involved. Vegetable tannins (or plant polyphenolics, Haslam 1989) are secondary metabolites of plants. They are defined as water-soluble phenolic compounds having molecular weights between 500 and 3000. By definition tannins also combine with protein, often irreversibly, and prevent the action of protein-digesting enzymes. They may also form complexes with other macromolecules, such as polysaccharides, and with alkaloids. Another property of tannins is their astringency, probably caused by combination with

proteins and mucopolysaccharides in the lining of the mouth (Harborne 1982; Haslam 1989).

Two major groups of polyphenolics are recognised, the proanthocyanidins, often known as condensed tannins (which may have higher molecular weights than the definition given above, and which are oligomers); and what are often known as the hydrolysable tannins, which are polyesters of simple phenolic acids (principally gallic acid - the gallotannins, or galloyl esters; and hexahydroxydiphenic acid - the ellagitannins or hexahydroxydiphenoyl esters), and their derivatives, with glucose (Harborne 1982, 1984; Haslam 1989). Condensed tannins are flavonoid based, while hydrolysable tannins are carbohydrate based (Hagerman and Klucher 1986). This second group is limited to relatively few dicotyledonous plant families (Harborne 1984).

2.3. TANNINS IN OAKS

Both groups of polyphenolics are found in various tissues of *Quercus* species, including acorns (see, for example, Koenig and Heck 1988); but the hydrolysable tannins are more common. Most early studies concentrated on parts of oaks used in the tanning of animal skins, but more recent work, especially in Japan, has examined other tissues, though not usually acorns (see Haslam 1989).

The association of oaks and tannins is a long one, and the word tan is said to be derived from the Celtic word for oak. 'Gallic' acid derives from its presence in galls, especially those of *Q. infectoria*, commercially known as Aleppo or Turkey galls (Haslam 1989). Other commercial sources of tannins derived from oaks have included the bark of young oak saplings (especially in Britain, where both *Q. robur* and *Q. petraea* were used, and which may contain 12-14% tannin - Howes 1974); wood; the cupules of *Q. ithaburensis* ssp. *macrolepis* (known as Valonea, which may be 36-58% tannin, Mabberley 1987); and roots of *Q. coccifera* (known as Garouille). The specific tannins in each of these sources vary in their chemical composition, and have been given names such as Turkish or Aleppo, Valonea, and oak gallotannins (Haslam 1989). All are hydrolysable tannins, as are the principle tannins isolated from the leaves of oaks.

2.4. EFFECTS OF TANNINS ON METABOLISM

The following account, except where indicated, is taken from Haslam (1989).

2.4.1. Toxic effects

The extent to which tannins, or more particularly those found in acorns, are toxic, is uncertain. Singleton (1981, cited in Haslam) concluded that polyphenols were only harmful in unusual and unpredictable circumstances. Liener's (1980) overview of toxins in plant foodstuffs records the major effect of tannins (principally condensed tannins) in vertebrates as depressing growth. Waterman (1988) summarised findings on the experimental effects of tannins on vertebrate and invertebrate metabolism, and concluded that the findings so far were ambivalent with regard to toxicity and anti-nutritional effects. Nevertheless, toxic effects of excess consumption of acorns have been recorded, principally among livestock (Cooper and Johnson 1984; North 1967), and Burkill (1935) reports various ills and a malady called "trousse galante" following their consumption by people during a famine in France.

2.4.2. Anti-nutritional effects

Tannins in general are thought to inhibit the digestion of proteins by binding with them, and it has been thought that this, together with their astringency, is the mechanism by which they act as anti-herbivore agents. Studies of oak-leaf tannins by Feeny (1968, 1969, 1970, all cited in Haslam 1989) suggested that tannins inhibited the digestive enzymes (principally trypsin) of insect feeders. However, more recent studies of tannins in oak leaves (Martin and Martin 1982, 1983, cited in Haslam 1989), provided little support for the view that variations in tannin levels between species have substantial effects upon digestibility of leaf proteins under conditions normally found in insect guts. Though some polyphenols undoubtedly do have the effect of inhibiting proteolytic enzyme activity, Haslam's re-analysis of the work of Feeny suggested that the major effects on insect metabolism were the appearance, at a certain stage of development, of proanthocyanidins, which are less astringent than other polyphenols, but bind strongly with plant tissue and increase leaf toughness. Other recent work has suggested that those tannins which are most soluble in water, including vescalagin and castalagin (ellagitannins) found in *Quercus* and *Castanea* have a weaker affinity for proteins than those that are poorly soluble in water (as are some of the galloyl esters). Hagerman and Klucher (1986) examined experimentally tannin-protein interactions. They cited some studies which found condensed tannins to bind more strongly with protein, others hydrolysable, and others that certain proteins bind strongly with both. Their own studies found condensed proteins to bind most strongly. They also examined the effects on different proteins, and concluded that interactions were very protein specific, but not tannin specific. Condensed tannins were slightly more effective protein precipitants. Proline-rich proteins had a particularly high affinity for tannins. New findings on the effects of tannins on animal metabolism are appearing

regularly, however, and there is little consensus on the precise mechanisms leading to anti-nutritional effects (Waterman 1988).

2.4.3. Other effects of tannins

One of the harmful effects of human consumption of tannins (from non-acorn sources) which has been recorded is the association with cancers of the digestive tract, notably in parts of the world, including eastern Turkey and northern Iran, where tannin-rich herbal teas are drunk. Tannins are not thought to be the direct cause of this, but to facilitate the action of carcinogens by damaging the mucous membranes.

Conversely, many medicinal uses of tannins of various origins have been recorded, especially from Japan and China where the effects are being investigated intensively. Some of the principal uses, especially of oak tannins from bark and galls, are in treating stomach disorders such as dysentery and diarrhoea. The medicinal effects of tannins in this case are thought to arise from the property of binding with proteins of the mucous and surface epithelial cells of the gut, producing an impervious layer under which natural healing can occur, and which can protect the underlying mucosa from toxins and other bowel irritants. Some tannins may also be anti-inflammatory; and numerous other uses and potential effects are listed by Haslam (1989).

Polyphenolics are toxic to various micro-organisms (Harborne 1982) and they have some anti-fungal effects, e.g., against *Fusarium*, though *Aspergillus* and *Penicillium* can stand concentrations of 2% or more tannin and can use hydrolysable tannins as a source of carbon for growth. They also have antiseptic properties (Harborne 1982).

Although tannins in fodder crops generally have a bad reputation, even here they may have beneficial effects. Bloat in ruminants is correlated with the absence of tannins, especially in leguminous crops, and the presence of tannins is thought to inhibit the microbial organisms, and the deleterious proteins produced by them, which cause the characteristic excessive fermentation or foaming (Harborne 1982).

APPENDIX 3. THE ACORN CROP - FACTORS AFFECTING ACORN PRODUCTION

3.1. INTRODUCTION

Because oaks and their acorns are such an important part of many ecosystems, especially in temperate forest regions, acorn production, and the factors that affect it, have been been studied in some detail. Much work has been done in North America particularly, principally by foresters and wildlife managers. There is some consensus on the general characteristics of acorn production, but, despite a great deal of study of many aspects of acorn production, no definitive conclusions have been reached about the degree to which different factors have an effect. In particular, the extent to which behaviour is genotypic or phenotypic - either as an innate physiological response to long-term environmental factors, or as an immediate response to local environmental factors - is much debated.

In the following discussion the processes that occur at each stage of acorn production, and the factors that affect these processes, is first described. Causes of variation in acorn production, between individual trees, populations, or species, and years, is examined next. Appendix 4 deals with the factors that affect the acorn crop, principally losses of acorns to insects, disease, and mammalian and avian predators.

As with all aspects of acorn biology the information is very much biased towards that from Europe and North America, as this is where the most detailed studies have been undertaken. However, because oaks in many ways dominate the ecosystems they are part of, and because the major ecosystems containing oaks are similar to those described here, it is not unreasonable to extrapolate at least some of the general principles indicated to other regions.

3.2. THE PROCESS OF ACORN PRODUCTION

3.2.1. Introduction

The processes of acorn production obviously relate very closely to the reproductive cycle of oaks. In this section each relevant part of this life cycle is described, in relation to its effect on the final acorn crop.

3.2.2. Flower bud initiation

The first factor of importance in acorn production is the laying-down of flower bud primordia. Without these the process can go no further.

3.2.2.1. Timing

In at least the temperate deciduous oaks, male flower buds are initiated in July of the year preceding flowering, with female buds forming later in the summer, perhaps even into autumn (Kaul 1986; Longman and Coutts 1974).

3.2.2.2. Factors affecting flower bud initiation

Matthews (1963) discusses the role of temperature, light, water supply, nutrient availability, and growth regulators in flower-bud initiation in forest trees in general and all no doubt have some influence in the oaks. In the British oaks hot, dry early summer conditions, and warmth later in the summer seem to favour the laying down of flower primordia (Evans 1988; Jones 1959). In general, though, the factors controlling flower-bud initiation and its variability have been little studied in comparison with later aspects of oak life history relevant to the production of acorns (Feret *et al.*. 1982). The numbers of flowers produced in any year presumably relates directly to the number of flower primordia laid down in the previous year, though there has been no study of the extent to which environmental or physiological factors might alter this.

It is possible that the crop of acorns produced in any year may influence the laying down of primordia, since growth of the acorns and initiation of the next year's buds take place at the same time. This aspect is discussed in more detail below (in 3.3.2.5.2.) because it is of particular relevance to year-to-year variations in the quantities of acorns produced.

3.2.3. Flowering and pollination

Quercus species are anemophilous, monoecious, and more or less self-sterile. Pollen is produced in vast quantities in favourable years (Jones 1959). Factors which affect the production and dispersal of pollen are obviously of considerable importance with regard to the subsequent crop of acorns, and have been studied in detail in Pennsylvanian white oaks by Sharp and Chisman (1961).

Male flowers are borne in the pendulous catkins which form within axils of leaves or bud scales of the terminal bud, or special buds on one- or two-year old wood. The female

inflorescences appear in the distal leaf axils, are few-flowered, with flowers solitary within individual cupules (Irgens-Moller 1955; Kaul 1986; Langdon 1939). Floral development has been studied in few oak species, mainly in temperate species, though in the most recent review Kaul (1985) examined non-temperate members of the genus as well.

3.2.3.1. Season and timing of flowering

3.2.3.1.1. Control of flowering

Flowering and pollination takes place early in the year in both temperate and tropical zones (Kaul 1985, though there may be some exceptions - see 3.2.5.1.), and appears to correlate with the time of first flush of leaves in temperate deciduous species, which in turn is controlled by factors relating to weather, site factors, and heredity (Irgens-Moller 1955; Longman and Coutts 1974). Some species of oak are protogynous, while others are protandrous (Camus 1936-1954; Irgens-Moller 1955). Timing of pollen-shedding is important because the period of receptivity of the female flower may be quite short (Irgens-Moller 1955; Jones 1959). In one study of the protandrous *Q. alba*, pistillate flowers appeared about 5-10 days after the emergence of male catkins, with shedding of pollen a similar number of days later. The timing of catkin emergence seems to be advanced by early warmth, with pollen dispersal then delayed by subsequent cool spells to coincide with pistillate flower development (Sharp and Sprague 1967). Sharp and Chisman (1961) found that in humid conditions the anthers remained closed and prevented loss of pollen, so that humidity regulated the time of pollen shedding.

3.2.3.1.2. Variation in flowering time

Precise timing of appearance of staminate catkins and pistillate flowers may vary from year to year and place to place within species, and may be influenced by weather conditions (Jones 1959; Sharp and Sprague 1967) or by responses to environmental variables. Neilson and Wullstein (1980) in a study of *Q. gambelii* found that a May freeze affected acorn production on low-altitude acorns, but not on those at high altitude, or low-altitude trees in frost-hollows, which delay staminate flowering. A later freeze in June gave low productivity at high altitudes where the flowers were just opening but good productivity at low altitudes, where the frost was not so intense, and where the young acorns were already developing and were perhaps less sensitive than catkins. Sharp and Chisman (1961) also noted variation in timing of staminate flowering in *Q. prinus* and *Q. prinoides* in relation to altitude and frost hollows, but in *Q. alba* hereditary differences over-rode these effects and produced 'flowering waves' of early- to late-flowering individuals, which however also varied in their precise timing from year to year.

Variation in the length of time over which pollen is discharged during any one year may also vary between trees of one species (e.g., from around 5-11 days in *Q. petraea* and *Q. robur* (Jones 1959), though most pollen is usually shed in the first few days. Because of this inter- and intra-populational variation in the timing of flowering, the pollination season of any one species may last several weeks in a given area.

3.2.3.2. Factors affecting flowering and pollination

3.2.3.2.1. Factors increasing pollination success

Sharp and Sprague (1967), in a 13-year study of flowering and fruit production in white oaks of Eastern North America, studied several environmental factors which had been suggested previously as having an effect on poor seed production in oaks and other trees. They found that the most significant factors appeared to be temperatures during the time leading up to flowering. A rapid early increase in temperature from mid-April, followed by a decrease in early May coincided with good production years, while a steady increase in temperature from April to May coincided with poor years (pollen shedding occurred from mid- to late May). It seems likely that these favourable conditions relate directly to the flowering and pollination period, almost certainly via their effect on the co-ordination of pistillate-flower receptivity and pollen release as described above.

3.2.3.2.2. Factors decreasing pollination success

Adverse conditions at flowering time may have an effect on subsequent acorn production, though in anemophilous trees in general pollen dispersal can occur very rapidly once conditions are right (Matthews 1963).

In conditions of prolonged and heavy rain the male catkins may fall before releasing their pollen (Sharp and Chisman 1961), and high humidity at time of flowering has been suggested as possibly having an adverse effect on pollen dispersal (Wolgast and Stout 1977b). Strong dry winds and high daytime temperatures may desiccate catkins and cause premature pollen shedding (Sharp and Sprague 1967).

Flowers are particularly vulnerable to frost damage both before and during the pollination period (Downs 1949; Goodrum *et al.*. 1971; Gysel 1958; Jones 1959; Neilson and Wullstein 1980; Nixon *et al.*. 1975; Parsons 1962; Wolgast and Trout 1979; Korschgen 1981), and severe frost around time of flowering may destroy a whole acorn crop (Sharp and Sprague 1967). Parsons (1962) noted that in *Q. suber* and *Q. faginea* the flowering

period is longer than that of *Q. ilex*, and these species are consequently less likely to suffer crop failure due to cold spring weather.

Other factors which may destroy flowers or impede pollen dispersal include hail, high winds, and biotic factors such as caterpillars or squirrels which eat the flowers (Evans 1988; Jones 1959; Havera and Smith 1979; Morris 1974; Nixon *et al.* 1968; Parsons 1962). The larvae of gall-midges (Cecidomyiidae), gall-wasps (Cynipidae), and of weevils (Coleoptera) may also attack flower buds and catkins (Morris 1974).

3.2.4. Fertilization

3.2.4.1. Timing of fertilization

A delay between pollination and syngamy is characteristic of the Fagaceae (Wigston 1974), and there is a distinctive difference in the length of this delay between some of the oak sub-generic groups (Conrad 1900; Irgens-Moller 1955; Kaul 1986). In sub-genus *Quercus*, the *Cerris*, *Erythrobalanus* and *Protobalanus* groups exhibit delayed fertilization - the pollen tube grows until it reaches the base of the style, and remains there until the following spring when completion of growth and fertilization takes place, though the exact time between pollination and fertilization may vary by a few months (Wigston 1974). In sub-genus *Cyclobalanopsis*, and in the *Lepidobalanus*, *Macrobalanus* and *Mesobalanus* groups, the pollen tube grows directly through the style until the ovule is reached, but there may still be considerable variation in the time between pollination and syngamy, as the period of growth may vary. Sharp and Sprague (1967) noted that American and European studies had produced differing results, varying from immediate fertilization to a period of a month or more, and according to Irgens-Moller (1955) growth may take up to 2 months.

3.2.4.2. Factors affecting fertilization success

3.2.4.2.1. Inherent factors

One experimental study involving grafted clones of *Q. alba* (Farmer 1981) found that while the most significant factor involved in year-to-year variation in acorn production was the number of flowers produced, variation between clones was most closely correlated with the numbers of flowers fertilised (defined as those not aborted by June), which therefore appeared to be under genetic control. Sharp and Sprague (1967) found that in years of low acorn production many female flowers developed with abnormal stigmas. However, they do not discuss whether these flowers were able to be pollinated, nor at what stage they aborted.

3.2.4.2.2. Environmental factors

One significant factor affecting adequate fertilization is pollen viability. Pollen of hybrid trees tends to be less viable than that of non-hybrids, a factor which is used to help differentiate hybrids (e.g., Rushton 1978). However, Sharp and Sprague (1967) suggested that pollen viability might also be influenced by environmental factors, and it appeared to be increased by a warm period prior to pollen release. Pollen viability during a year of good acorn production was over 85%, but they did not report viability in any of the poor production years.

Because of the often considerable time between pollination and syngamy it is likely that environmental factors are important in affecting fertilization. However, this aspect of oak reproduction has been little studied, and in any case it would be difficult to distinguish between factors which prevented fertilization, and those which caused abortion of young developing acorns.

3.2.5. Acorn growth and survival

Once fertilization, or fruit set, has taken place, the future of the acorn crop is still by no means certain, as a considerable period of growth and ripening must elapse before dispersal in the autumn.

3.2.5.1. Acorn growth

Some oaks produce acorns within the year of flowering, others in the autumn of the following year. In two-year oaks, there is a delay in fertilization from time of pollination until the following spring (as described above - 3.2.4.1.), though there are some exceptions within the groups listed. *Q. suber*, for instance, a member of the two-year *Cerris* group, ripens acorns in the first year in spring-flowering trees, but has some trees which flower in autumn, with acorns ripening late the following summer (Tutin *et al.* 1964). In any case the process of acorn growth takes place during the year of maturation, and there should be little difference in its effects between the two groups. However, the fact that unfertilized embryos of the two-year oaks are present on the trees for approximately a year before the process of growth begins means that there may be additional factors involved in their survival.

Smith and Scarlett (1987) however, who analysed data collected on a very large scale on production of acorns (and of other nut-producing species - *Carya* and *Juglans*) over a period of between 5 and 24 years over a large part of Missouri found that there was a close

correlation between production of acorns in the red and white oak groups. They suggested that environmental conditions during the developmental year were more important in determining red oak mast production than conditions experienced during flowering and fertilization in the previous year.

3.2.5.2. The process of acorn growth

Once fertilization has been completed successful female flowers enter a developmental phase, which is discussed in some detail by Kaul (1986), Langdon (1939) and Sharp and Sprague (1967). The timing of stages within development varies between species growing together, and also within species in relation to environmental factors due to latitude and altitude (Sharp and Sprague 1967). Sharp and Sprague suggest that conditions conducive to good or poor acorn production apparently begin early in the year. An important factor seems to be rapid early growth of the peduncle, which provides the route by which nutrients reach the developing embryo. They found that there was poor early growth of peduncles in poor years, and rapid early development in years with heavy yields (Sharp and Sprague 1967).

3.2.5.3. Abortion of immature acorns

In oaks very large numbers of developing acorns are aborted, even in years with high acorn productivity (Christisen 1951; Downs 1944, 1949; Feret *et al.* 1982; Gysel 1958; Matthews 1963; Shaw 1974; Tryon and Carvell 1962; Wood 1938). The greatest percentage of these premature abscissions appear to take place during pollination and fertilization (Feret *et al.* 1982), but there are still significant abortions later in the season, and it may be that some unfertilized or self-fertilized acorns will remain on the tree until the fall of ripe acorns, as seems to be the case in hickories. In *Carya glabra*, fruits infested by weevils and some aborted fruits fall mainly over the summer. Fruits in which the embryos have aborted may continue to grow so that they appear externally similar to viable fruits (Boucher and Sork 1979).

Where female flowers are in groups in one axil frequently only one will mature, except in years with heavy production. Abortion of acorns seems to relate to position on the shoot, and Sharp and Sprague (1967) found those in the axils of lower leaves dying first (as early as May) while those in the upper axils aborted in June, and sometimes as late as early August. Jones (1959) comments that the apical acorns in an inflorescence usually remain smaller than the lower acorns. In *Q. robur* he noted that these usually aborted early, while in *Q. petraea* the upper acorns tended to persist in growth.

3.2.5.4. Factors affecting acorn growth and survival

Some authors, including Tryon and Carvell (1962) have noted that certain trees regularly produce a higher percentage of immature acorns, suggesting a hereditary influence on the likelihood of subsequent growth. To what extent immature acorn abortion is due to failure in pollination or fertilization (e.g., by self-fertilization), or is due to physiologically or environmentally induced factors which affect successfully fertilized acorns is uncertain, especially as most studies of losses at this stage do not differentiate between 'sterile' acorns and those which are merely immature. Because of a longer period of development in the red oaks and others which take two years between flowering and acorn maturation (see above, 3.2.4.1. and 3.2.5.1.) it is possible that these could be more vulnerable to environmental influences, but there is little documentation of this. Gysel (1958) found that losses of immature red oak acorns appear to be minor over the winter, but that there may be large losses of immature acorns during their second summer, i.e., that leading up to their maturation. However, he could determine no reason for these losses.

Environmental factors certainly have some influence on acorn growth and development. In Britain many acorns may fail to mature, or will be smaller than average, in cold summers (Jones 1959). Though the young developing acorn is perhaps less vulnerable to damage than the flowers of the oak, a crop can nevertheless be severely depleted at this stage - in one year in southeastern Ohio a severe frost after seed development had begun totally eliminated crops in the white oaks, and damage was severe enough to kill most of the developed embryos on red oaks, so that only light crops were produced in that year (Nixon and McClain 1969). Downs (1949) also notes that late frosts or other bad weather conditions may destroy fruit in the young tender stage, and that some acorns may abort due to early insect damage, and Schettler and Smith (1980) noted that in California oaks the first wave of falling acorns consists primarily of aborted and weevil-eaten acorns.

3.2.6. Maturation of acorns

The process of acorn maturation is described by Sharp and Sprague (1967). Acorn fall and dispersal and its timing is likely to be of considerable importance to exploiting human populations. There may be differences between species, as well as inter- and intra-populational variation in the timing of fruit-fall, relating to both genotype and environmental factors.

3.2.7. Period of ripening of acorns

Information on the average time of dispersal of acorns is provided in some floras and plant manuals (e.g., Sargent 1905; Scott and Parkinson 1930), though many do not include this type of information. Again, studies by foresters and wildlife biologists are the best sources of information. For example, Van Dersal (1938) gave the average time of ripening of many North American species, with the earliest in September. The majority of species are listed as available from September to October, or October to November, though a few have longer or shorter periods of availability. Average times of ripening of oak species planted in the British Isles are given in Gordon and Rowe (1982).

Parsons (1962) states that in Southwestern Spain the period of bearing varies, apparently consistently, between three species, with *Q. faginea* earliest, *Q. ilex* from October through January, and *Q. suber* from mid-September through early February. Similarly in Arizona Eddy (1961) noted ripening of acorns of *Q. emoryi* from July onwards, while other species became available from October onwards. In the Ozarks Burns *et al.* (1954) and Christisen (1955) suggested that acorns of the red oak group appeared to continue falling for longer than those of the white oaks, especially *Q. marilandica* which continued to drop acorns through the winter. Lewis (1982), however, found that *Q. alba*, *Q. prinus* and *Q. rubra* fell over a similar period and at a similar rate in one year between early September and late October. Park (1942) in a four year study including six oak species, noted no more than 15 days variation between years, from the first to the second week in October in date of first ripening. Species varied by from six to 30 days in the date of drop of the last of the crop, but variation did not correlate with oak group. Griffin (1971) recorded time of ripening for five Californian species over three years. In all three years the first species dropped in mid-October with the last species to ripen varying between years from early to late November. Individual species did not always ripen in the same sequence each year, though, over the period studied, *Q. kelloggii* was always among the first to ripen (in the two years in which it produced any crop), and *Q. agrifolia* was always the latest.

Jones (1959) comments that intraspecific variation in period of acorn drop exceeds interspecific variation in the case of the two northwest European species, *Q. petraea* and *Q. robur*. On average fruiting begins at the end of September/early October, though most of the early ones are empty or infested, and most sound acorns fall in mid-October. Late individuals may be dropping acorns into the second week of November. Similarly, Cypert and Webster (1948) noted that, though most trees produced some acorns over the period from early September to December, there was considerable variation in time of peak drop of individual trees, ranging, in a year of heavy crop, from around September 1st to November 23rd, in a year of low crop, from September 15th to the end of October, and for

an intermediate period in a year with intermediate production. The average peak for all trees combined varied between years from the last week in September to the third week in November.

Downs and McQuilkin (1944) also examined inter-annual variations in the period of ripening and availability of acorns, for five species combined. The period of first drop ranged from around the second week in August to about one month later, with peak availability ranging from the third week of September to the end of October. There is a considerable range in the time during which acorns may remain on the trees, and Burns *et al.* (1954) and Christisen (1955) found in their study in the Ozarks that in years of heavy crops the period of drop lasted slightly longer. Koenig and Mumme (1987), however, examined the period of retention of acorns on Californian oaks, and found it not to correlate with crop size.

There may be variation in time of drop between sites. The study by Burns *et al.* (1954; see also Christisen 1955) found acorns beginning to fall in August at two sites, though at this time primarily as immature acorns, while at another site acorns did not begin to fall until October. They noted that climatic factors such as heavy rain, wind, or frost accelerated acorn drop. Other studies have noted that the earliest acorns to drop are often sterile or insect-damaged (see Jones 1959, above, also 3.2.5.4., above). Menke and Fry (1980) recorded immature or insect-damaged acorns of three Californian species beginning to fall from May to July, with sound acorns falling in late August, and the majority in October and November.

The period during which acorns are available is likely to be of considerable importance to exploiting human populations, and this factor is discussed further in Appendix 4, 4.5.

3.3. VARIABILITY IN THE PRODUCTION OF ACORNS

Variation in production of acorns occurs on a number of different levels, the principal ones being variation between species, between individuals or populations within species, and between any of these groups over time. Some indication of the kinds of variations that exist between species can be seen in Table 14, and are discussed further in Chapter 7.

Though variability is usually discussed in terms of the numbers of acorns produced this is not the only kind of variation. There may also be differences in seed size from tree-to-tree and year-to-year, which may be as much as 150% of the average weight of a seed between years (Brookes and Wigston 1979; Jones 1959; Koenig and Mumme 1987).

Variability may be due to innate influences (physiology or genetics), or to environmental effects on flower production or fruit growth (Feret *et al.* 1982). It is very difficult to separate the effects of the different causes of variability in acorn production. As Sharp and Sprague said: 'Hereditary and other influences operating within individual oak trees present numerous unsolved problems. The combined results of hereditary or physiological influences make it difficult to determine which factors are responsible for the regular fruitfulness or non-fruitfulness of the trees' (1967, 250).

3.3.1. Variation between trees

In this section variations in productivity within species, and the likely causes of this, is discussed.

3.3.1.1. Hereditary effects

There is no doubt that there are significant genotypic differences in productivity potential between different trees, a not surprising fact considering the great degree of inherited variation present within the oaks (see 4.3.4.). To quote Sharp and Sprague: 'Acorn yield in individual white oak trees is so constant that the potential appears to be a hereditary characteristic. Without man's selection, a white oak community consists of trees ranging from low to high fruiting potential...in years with heavy white oak acorn yields some trees produced no acorns; others nearby produced poorly; in contrast, on the same site, still others produced good crops of acorns. In good years, one tree that produced a heavy crop of acorns did so consistently; an adjacent tree was a poor acorn producer over the 13-year period. Fruiting potential, apparently an innate characteristic of each tree, showed a wide range, even among open-grown trees with dominant crowns' (Sharp and Sprague 1967, 250). They found that within one species, production by individual trees varied from as much as 300 lbs of acorns, to less than 10 lbs/tree. Many trees produced few or no acorns throughout the period of study. They found this kind of variability in yield from tree to tree in all the species they studied.

Similar observations have been made by many others including Brookes and Wigston (1979), Burns *et al.* (1954), Christisen (1955), Cypert and Webster (1948), Downs and McQuilkin (1944), Downs (1949), Goodrum *et al.* (1971), Gysel (1956), McClennen (1939, cited in Van Dersal 1940), Parsons (1962), Passof *et al.* (1985), Petrides *et al.* (1953), Smith (1929), Tryon and Carvell (1962), Wood (1934, cited in Van Dersal 1940), and Wood (1938) and in some cases transplantation experiments have provided support for the inherited nature of some variability (e.g., Wolgast 1978). An experimental study involving grafted clones of *Q. alba* (Farmer 1981) found that there were significant

differences in yields over four years between the clones, which apparently related to fertilization success.

The importance of the effect of genotype may vary between species. Tryon and Carvell (1962) noted that the hereditary effect on acorn production seemed to be greater in *Q. alba* than in *Q. rubra*. Individuals of *Q. alba* tended to be more consistently good or poor producers, while *Q. rubra* individuals did not vary so much.

3.3.1.2. Effects of tree characteristics

As is implied by the previous section, it may be that hereditary influences, and variability induced by climatic factors over-ride the effects of other tree characteristics, but these certainly have some part to play in variation of yields between trees.

3.3.1.2.1. Effects of age

Flowering, and fruiting, in young trees tends to be sporadic, but increases rapidly with age - older trees (up to the age of decline) tend to produce more acorns, related partly to their increased crown volume (Goodrum *et al.* 1971; Matthews 1963). As trees become old yields may become small or negligible (Evans 1988; Passof *et al.* 1985), partly related to death of older portions of the crown (Goodrum *et al.* 1971). The age at which fruiting declines may, however, also vary, partly depending on local conditions (Jones 1959).

The age of first fruiting in oaks varies greatly between the tree and shrub oaks. In the larger, and generally longer-lived, tree oaks, at least those in Europe, flowers may not be formed until at least the age of 20-30 years, and it may not be until the age of 40 or more that substantial fruit production occurs (Longman and Coutts 1974). However, some species may produce acorns in large numbers earlier than this, e.g., *Q. rubra* (planted in Britain) has produced large quantities of fruits by the age of 30 or earlier (Jones 1959). Many of the American species begin bearing fruit around 20-25 years old, though optimum seed-bearing age may be much later (Fowells 1965; USDA 1974). Tree oaks such as *Q. nuttallii* may fruit as early as 5 years old, and *Q. virginiana* also fruits at an early age (Miller and Lamb 1985). Generally though, flowering tends to occur earlier in the shrub oaks, possibly related to their shorter lifespan (Waller 1979). A pot-grown specimen of *Q. pumila*, a small shrub oak of the American southeast produced acorns as little as two years after germination (Allard 1940). Differences relating to acorn production between tree and shrub oaks are discussed in 4.6.4.

Though age of first flowering tends to be relatively consistent within species, their may be variation due to either environmental conditions or genotype (Matthews 1963); and Smith (1929) notes many examples of abundant precocious fruiting by individuals. Although most authorities give age of first fruiting in *Q. petraea/robur* as 40-50 it has been recorded in southern Europe at 30-35, and it is likely that fruiting generally occurs earlier in warmer climates (Jones 1959). Trees on warm south-facing slopes, in the open or in edge habitats will fruit at an earlier age than north-facing, shaded or closed-stand trees (Jones 1959; Matthews 1963). Trees which grow rapidly, and coppice shoots, may fruit earlier than others (Evans 1988; Shaw 1974). The effects of coppicing on acorn production are discussed further in 4.6.4.

Goodrum *et al.* (1971) noted that a larger percentage of larger trees produced acorns, suggesting variability in the age at which trees come into production, probably related to genotype.

3.3.1.2.2. Effects of tree size

There seems to be a general relationship between acorn productivity and crown size, as noted by Burns *et al.* (1954), Downs (1944, 1949), Downs and McQuilkin 1944; Goodrum *et al.* (1971), Matthews (1963), Passof *et al.* (1985), Petrides *et al.* (1953), and Tryon and Carvell (1962).

This relationship sometimes also holds for stem diameter (Downs and McQuilkin 1944; McQuilkin and Musbach 1977), principally as it is usually closely correlated with crown area. Tree height has a much smaller effect on acorn production than diameter. The reasons for increased acorn production by trees with greater crown volume, is partly related to the greater potential numbers of shoots available, on which acorns may be borne (Matthews 1963; Petrides *et al.* 1953).

Cypert and Webster (1948) and Tryon and Carvell (1962) have both noted the effects of tree size on acorn production, but also commented that there is great variability within size classes, presumably due to hereditary factors.

3.3.1.2.3. Effects of tree health

General tree health is probably important in controlling how successful a tree is at producing acorns, though where a tree is in decline seed production may temporarily rise as a stress response (Evans 1988). Acorn crops in Britain may be reduced by the attack on their foliage of the oak mildew (Murray 1974).

Goodrum *et al.* (1971) examined the effect of relative growth rates on acorn production, but concluded it was not a good indicator of yield potential, though, Cypert (1951, cited in Goodrum *et al.* 1971) had discovered a relationship in *Q. falcata* var. *pagodaefolia.*

3.3.1.3. Effects of environmental variables

Some studies have compared the relationship of different 'site' qualities to variable acorn production. Site indexes may be produced relating to many different factors, including aspect, slope, edaphic factors, water table, and rainfall. The effects of these combined environmental characteristics may then be compared with variation in production of individual trees. These studies have indicated that there is usually less variation attributable to such site characteristics than there is to individual variation between trees on similar sites (Christisen and Korschgen 1955, cited in Goodrum *et al.* 1971; Cypert and Webster 1948; Downs and McQuilkin 1944; Sharp and Sprague 1967; Tryon and Carvell 1962). These results suggest that genotypic factors are of over-riding importance. Nevertheless, despite these generalised findings, there is much evidence that such environmental characteristics may have a significant modifying effect on acorn production by individual trees.

Environmental variables may be of relevance on a number of different scales. Large-scale differences in environment may be of particular importance when considering variability in acorn production in different localities of members of widely-distributed species. These differences might be largely differences in climate or soil type or topography and physiography. Such variations can occur over small areas too, and very local differences may be involved, such as the position of a tree in relation to others and to its accessibility to warmth, light, nutrients, water, etc., as well as its exposure to local climatic vagaries. The effects of these spatial environmental variables may be interrelated in a complex way and it may be difficult to separate the effects of differing environment from the effects of the genotypic differences which are so important in the oaks, and are particularly so when considering widely-distributed species. Nevertheless, some general conclusions can be drawn.

3.3.1.3.1. Effects of climate

In Scotland and Ireland acorns are usually smaller than in southern England, and there may be more frequent crop failures (Jones 1959). Both these differences are likely to relate to climatic differences between these areas, such as cooler summers, or more frequent destruction of flowers and young acorns by vagaries of weather.

Climatic changes associated with topography may also explain variation in production from place to place. The effects of frost seem to be particularly important in relation to acorn production, and prolific seeding may vary between valley stands and hilltops owing to frost (Evans 1988; see also this Appendix, 3.2.3.1.2., 3.2.3.2.2., 3.2.5.4.). Differences in production of acorns between individuals or localities could be produced by local variations in any of the factors which are of importance in the processes of acorn growth, described in this Appendix, 3.2.

3.3.1.3.2. Effects of edaphic factors

Although many workers have recorded that the effects of 'site' seem to be of less importance in controlling variability in acorn production than other factors (see this Appendix, 3.3.1.3.), some have found correlations between productivity and soil quality. Petrides *et al.* (1953) found decreased production by *Q. stellata* on poorer soils in East Texas - the trees themselves were smaller in such conditions. Wolgast (1978) measured the effects of water table depth, various inorganic soil constituents, organic matter and soil texture on high, low, and medium-producing trees and found that together these accounted for around 25% of the variation; and Wolgast and Stout (1977a) also found that acorn production by certain age groups of *Q. ilicifolia* could be increased by application of fertilizer, suggesting that soil fertility may have a significant effect on productivity. Gysel (1957) examined production by three species on sites of poor, medium and good soil quality. Though the results were difficult to interpret, because a different combination of species was present on each site, he concluded that there did seem to be a difference between sites of different quality in the total weight of fully developed acorns produced. However, this effect diminished when only sound acorns were considered.

Feldhamer *et al.* (1989) noted that the moisture-holding capacity of soils might modify the relationship between rainfall and acorn production, which they found to be significantly correlated over time.

McQuilkin and Musbach (1977) examined the effects of artificially flooding bottomland oaks during the dormant season, and found that this significantly reduced the yield of acorns, though a lower percentage of insect damage on these trees meant that a similar number of sound acorns resulted from flooded and unflooded sites.

3.3.1.3.3. Effects of tree position

Whether a woodland tree is a dominant or not, and the extent to which the tree crown is exposed to light, has a significant influence not just on the age of first-fruiting (see this

Appendix 3.3.1.2.1.), but also on average acorn production in any one year. Sharp and Sprague (1967) noted that trees with co-dominant or suppressed crowns in a canopy produced fewer good yields than those with dominant crowns. Oaks grown in the open produced acorns uniformly over their crowns, while those in closed canopy did so only on branches exposed to direct sunlight. Shade apparently curtailed acorn production on the lower branches of oaks of otherwise high fruiting potential. Gysel (1958) noted that the number of branches producing acorns was higher on open-grown and edge trees in comparison with numbers on interior trees, and also that there were greater numbers of branches on south-facing edges than north-facing, and it seems likely that acorn production would be correspondingly greater in response to this. Matthews (1963) considers that high productivity by dominant trees in forest stands is related not only to better exposure to light but also to their better opportunity to utilize nutrients.

Petrides *et al.* (1953) have similarly noted that large dominant trees are the main seed producers, and also that certain trees isolated in open pasture may produce very high yields even in poor years when very few acorns are produced elsewhere.

Several workers have noted that thinning of tree stands (which would produce greater exposure to light, increased growth to give larger crown volume, and less competition for nutrients) increases flowering and seed production (though not in all trees, indicating the over-riding importance of hereditary influences) (Evans 1988; Matthews 1963; McQuilkin and Musbach 1977; Sharp and Sprague 1967).

3.3.2. Temporal variation in acorn production

Year-to-year differences constitute a form of variation in productivity of acorns which is of great importance, and great complexity. Discussion of this aspect of acorn production has been left until last because it depends to a great extent on interactions between many of the factors already discussed.

Quercus is one of a large number of genera of trees which exhibit 'masting', or periodic variation in the quantities of fruit produced. The word 'mast' comes from the Scandinavian 'mat' meaning animal fodder, and originally related primarily to the fruits of beech and oak (Evans 1988), but the term has come to be expanded to cover all trees which fruit periodically.

The masting habit has been characterised as the synchronous production of seed crops at irregular intervals with an average periodicity characteristic of the species (Silvertown 1980). However, the extent of synchroneity and the average periodicity in oak species are

both variable features, depending on the scale at which they are examined, and while it is possible to make generalisations this variability must always be borne in mind. The question of how a mast year is defined may explain some of the variability in figures offered as being average periodicities for any one species. The term 'mast cycles' has often been applied to oaks and other masting trees, but Brookes and Wigston (1979) caution against the use of the term cycle since the occurrence of mast and blank years is irregular. It also obscures the extent of variability within masting itself, i.e., the extent to which there exist intermediate levels of production. In the literature the contrast between mast years and blank years tends to be over-emphasised and though there may be long intervals between exceptional mast years, years with heavier than average seed crops occur at more regular intervals (Evans 1988; Jensen 1982). There is, in fact great variation, from exceptional mast years through good, medium and low production, to years when there are no acorns - and this can apply to anything from one individual, through a population, a species, a sub-generic group, or to all species, and may or may not vary over the total area of distribution. Especially in areas where there are several species of oak present some acorns tend to be produced in every year in at least small quantities (Burns *et al.* 1954; Korschgen 1962).

3.3.2.1. Studies of masting in oaks

Despite the importance of acorns within ecosystems, and the correspondingly large amount of attention which has been paid to them, very little is really known either about temporal and spatial patterns of mast abundance or about the factors involved in producing variability in production over time. The situation has been studied most in eastern North America, and here the presence of two groups (the red and white oaks) with markedly different fruiting patterns, and of numerous species within each group, make for a complex situation. Many reports have been restricted in the areas covered, and in the time over which they took place, and there is very little known about correlations in production within or between species over wide areas. The situation in northern Europe is perhaps more easily assessed, because it focusses principally on only two species. Information on other parts of the world - southern Europe, the Mediterranean and Southwest Asia, Central America, and Southeast Asia is very sparse, if not non-existent. Most of this discussion is therefore drawn from the first two areas, and environmental differences must be borne in mind if extrapolating outside these areas.

3.3.2.2. Frequency of abundant acorn production

Most reported figures on the periodicity of acorn crops can be assumed to refer to the occurrence of abundant crops. Although a regular pattern of abundant crops does not usually exist (Burns *et al.* 1954; Goodrum *et al.* 1971; Gysel 1956), the average periods

have been determined in some cases. For example, long-term studies have demonstrated that in North America most species fruit abundantly every two to five years (Burns *et al.* 1954; Downs and McQuilkin 1944; Fowells 1965; Smith and Scarlett 1987). Not all species will necessarily vary in production from year to year. For example, Burns *et al.* (1954) noted significant variations in production for most species over six years, except in *Q. stellata*, where production remained very similar. Figures estimated for different species are presented in Table 14. In general most species do not produce abundant crops in consecutive years (Smith and Scarlett 1987), though again this is not always true.

The potential for temporal variability in oaks can be illustrated by that which has been recorded for *Q. petraea* and *Q. robur*. In Britain there are years in which heavy crops occur over large areas, and they occur about every six to seven years, but moderate crops occur every three or four years, and years in which there is a more or less complete failure are frequent. However, even in these years there may often be limited areas with heavy crops, and, conversely, in years of heavy crops there may be isolated areas where crops have failed. In France, heavy crops may occur every three to four years in some areas, with a gap of eight to ten years in less favourable areas. In some parts of the continent intervals of twenty to twenty-five years with only very light crops may occur. In Britain *Q. petraea* generally appears to fruit less frequently than *Q. robur*, but this may not be the case in every area, though variations from tree to tree, and between the habitats commonly occupied by the two species, make the situation difficult to estimate accurately (Jones 1959).

Occasionally there are years which are exceptional in their yields and extent. In France 1949 is considered the mast year of the century, and 1919 is sometimes similarly regarded (Evans 1988).

Not only do individual trees tend to produce more acorns in a good year, but there is a tendency for a larger percentage of oak trees to have acorns in good mast years (Goodrum *et al.* 1971; Smith and Scarlett 1987; Trail 1980).

3.3.2.3. Synchroneity

The masting situation in the oaks is particularly complex, since in many ecosystems in which they occur there may be numerous species, and within those species there may be genotypes which behave differently. There may be synchroneity of production within a population, an area, a species, or even between several species. The extent to which synchroneity of production within any of these categories occurs is partly dependent upon

the scale at which this is examined. Though there may be a widespread heavy crop, individual trees or local populations may be blank.

Across much of Europe, in some years, widespread synchronisation of good or extremely poor production of acorns (see this Appendix, 3.3.2.2.),which may also affect the beech crops over a similar area, has been recorded (Jensen 1982). However, synchronous production is not always the case, and Brookes and Wigston (1979) present some data indicating the variability in production between different sites in the same year.

Within the North American oaks some studies have suggested that there is sometimes synchroneity of abundant production between species, especially those in one or other of the red and white oak groups, and sometimes of members of both groups. Others have suggested that members of the two groups will synchronise their production in alternate years so that heavy yields are complementary. However, there is very little information regarding the geographical extent of any such synchroneity, complementarity, or other interspecific patterns of mast production, or whether it occurs in other parts of the world where there are one-year and two-year oaks.

The findings of the North American data that do exist are summarised here. Some studies have noted a tendency towards synchronous production, especially of heavy yields, by several species (sometimes including members of both oak groups), and sometimes for several localities, as did Burns *et al.* (1954) (see also Christisen 1955) in the Ozarks (looking at three sites over six years). Over three years Cypert and Webster (1948) found similar production by *Q. phellos* and *Q. nigra* (both *Erythrobalanus*). Sharp and Sprague (1967) noted that there were good and poor acorn seasons for two species of *Lepidobalanus* together (*Q. alba* and *Q. prinus*). Gysel (1956, 1957) found that two red oaks (*Q. velutina* and *Q. rubra*) had similar trends of production over five years, and that *Q. alba* followed this trend, except for two years when its crop failed. He did, however, note that production varied over space, and good yields in one place for one species could coincide with poor yields elsewhere.

Figures presented by Dalke (1953) showed that one year of simultaneously relatively high yields in six species was followed by a year of lower yields in most of these. Downs and McQuilkin's (1944) study of five species at two sites over seven years showed similar trends in production at both sites for each year, and they suggested, as did Burns *et al.* (1954), that production variations are regional phenomena. Goodrum *et al.* (1971) also noted a common trend (for seven species of both red and white groups over 18 years), with some years of generally high yields and some of generally low yields. However, they also noted that some species could have a good year when others were having a poor year.

Smith and Scarlett (1987) analysed data collected in Missouri over a period of around 30 years. Treating oaks as white and red groups they found that correlations, in heavy yields only, over the whole period and area, were statistically significant; but that general correlations in yield were not always to be found, and that, within any county sometimes one group had heavy yield while the other had low yield.

Several of those studies that have found such general synchrony have also pointed out that it is rare to have years of complete failure (either because a few acorns are produced by several species, or because one species yields heavily out of synch) (Burns *et al.* 1954; Goodrum *et al.* 1971; Korschgen 1962). Park (1942) however, found crops of five species (of both oak groups) all failing simultaneously in one year of a four year study, with two white oaks also failing simultaneously in the previous year. Despite their general finding of synchronous production Burns *et al.* (1954) emphasised the importance of maintaining several species in an area in order to avoid fluctuations in crops. The data presented in support of synchronous production (within or between species or groups of species) indicate that this is only a tendency and one species may produce well in one site and not another in one year, and one or more species may produce good crops when others are not.

Other data have been used to suggest that there may be complementarity of good and poor yields between years in the two oak groups present in eastern North America (which requires that there is some synchroneity within each group). Korschgen (1962, 1981) stated that the two groups usually do not produce heavily in the same year, but the qualitatively presented data he gave for two periods of three and five years nevertheless show some similar trends. Yield data presented by Tryon and Carvell (1962) over a six year study indicated significantly different annual production by *Q. rubra* and *Q. alba*, though their figures showed that in some years yields were very similar for the two species. They also felt, from observation of other species in the area, that usually at least one species would produce a good crop.

Most data are fairly ambiguous however. Nicholas and White (1984) presented qualitative indices for eight species showing that yields of red and white oak groups tended to follow a roughly similar trend over four years, though in one year red oak production was considerably better than for the white oak group. Within the groups, also, in some cases, some species had high yields while others had poor yields. Data obtained by Havera and Nixon (1980) for five species over three years showed, in some years similar trends in production between species, while in other years one species yielded heavily while another yielded poorly, irrespective of oak group. Data of Nixon *et al.* (1975), for red and white groups only, showed a similar pattern, with similar yields in some years and complementary yields in others. Henry and Conley (1972) presented qualitative data on

yields of red (three species) and white (four species) oaks over five years. For one year both groups failed, in another both groups produced few, while for the other three years the groups had roughly complementary yields.

One of the few published studies of annual yields from California is that of Griffin (1971), whose data over three years showed trends towards good and poor production in the same year for four species, with a fifth, *Q. kelloggii*, showing a complementary pattern. Interestingly, while three of the remaining species are members of *Lepidobalanus*, the fourth is *Q. agrifolia*, which is one of the few members of the red oaks whose acorns mature, like those of the white oaks, in one season. Verner (1980) based on observations of yields made by others in California suggested that different species tend to produce well in different years; but there is little further information on this area.

3.3.2.4. Ultimate causes of masting behaviour

The general nature of the masting habit, including the likely reasons for its evolution in certain types of trees, has been discussed by, amongst others, Harper and White (1974), Harper (1977), Janzen (1971), Jensen (1982), Matthews (1963), Silvertown (1980) and Waller (1979).

The most commonly-accepted explanation for the evolution of the masting habit in trees is its adaptive significance in relation to predation - what has come to be known as Janzen's (1971) 'seed-predator satiation strategy'. The synchronous production of large quantities of seeds increases the likelihood of some of those seeds avoiding being eaten and going on to grow into a new tree, and low production in intermediate years keeps in check the populations of predators which may have boomed following the mast year. For species which share the same predators (as the oaks generally do, and often also share them with others of the nut trees) there is a selective advantage in synchronising crops across the species boundaries (see also Fenner 1985).

It has been suggested that there may have been selection for characteristics of acorns in relation to their dispersing agents (see Smith and Follmer 1972). Kaul (1986) notes that predation and burial of mature fruits by large herbivores is often an essential part of the dissemination and germination of oaks, and despite the acorn's apparent defences at maturity (shells and tannins) these do not deter those animals. The potential role of animals in this respect is illustrated in more detail in Appendix 4.

Silvertown (1980) analysed some of the data on synchronous fruiting of oaks noted by various workers (see previous section), and examined the hypothesis that the fact that mast

years seem to be highly correlated with specific climatic conditions suggest that masting may simply be a consequence of environmental and physiological constraints on seed production. By examining the relation between crop size and subsequent seed survival he concluded that masting may have evolved in response to fluctuations in climate affecting crop size which were then magnified by strong selective pressures from seed predators. He concluded that it would be expected that synchrony would sometimes occur between members of different species of oaks, when they occur as sympatric populations.

Both Silvertown (1980) and Waller (1979) considered the relation of the masting habit to life history factors. Masting is considered likely to be less common in shorter-lived members of any genera, such as shrubs (Harper and White 1974). Although there is a general relationship when comparing many tree and shrub genera (Waller 1979), Silvertown (1980) could find no correlation between longevity and mast interval within the North American oaks. However, both workers also noted the generally smaller seed size found in shrubs, and the fact that *Quercus* contains non-masting species which have smaller seeds.

3.3.2.5. Factors affecting masting

It is difficult to separate factors which are responsible for acorn production and its variability from those which are responsible for periodicity of production - obviously the two are inter-related. Many of the factors that affect production and the reasons for its variability have already been discussed, so in this section the focus is on those factors that seem to be responsible for patterns of production.

Likely proximate causes of periodicity in fruiting in trees have been discussed and summarised by, among others, Baldwin (1942), Matthews (1963), Nixon *et al.* (1975), Sharp and Sprague (1967), Feret *et al.* (1982), Evans (1988), and there is a certain amount of consensus regarding the general factors involved.

Within any one species there are three major factors involved in control of production of acorns by any one tree: hereditary factors (genotype), physiological factors (the condition of the tree, which may partly relate to the extent to which a previous crop may have deleted reserves), and environmental factors. The latter can be divided into two: firstly local environmental/physiographic conditions which are unlikely to vary over the time scales being considered (edaphic, topographic, altitudinal, climatic, etc), and secondly those factors which may vary from year to year and affect acorn production on this basis (variations in 'weather', especially relating to extremes - of rainfall, temperature, etc., or in

the effects of insect predation on flowers or developing acorns, as well as the effects of disturbance).

3.3.2.5.1. Heredity

Heredity is undoubtedly important in controlling the extent to which acorns are produced by any one tree within a species (see this Appendix, 3.3.1.1.). This element is mainly expressed as variation between and within populations however, and it is difficult to relate it directly to temporal variation in production. Nevertheless, the fact that trees of one species tend to mast in a synchronous way indicates that there are hereditary factors involved in periodicity, and these almost certainly act through controlling responses to environmental cues (Silvertown 1980). Hereditary influences may modify environmental effects, for example by controlling the 'flowering waves' in *Q. alba* noted by Sharp and Chisman (1961) (see this Appendix, 3.2.3.1.2.), which could influence the likelihood of some members of a species avoiding the effects of, for example, killing frosts, and thus increasing the likelihood of some acorn production in each year.

One important modifying influence that hereditary effects might have was noted by Tryon and Carvell (1962). They found that differences between years in yields of *Q. rubra* were significant, while in *Q. alba* they were only nearly significant. In both cases, as noted in this Appendix, 3.3.1.1., there was more difference in production between individuals than between years, but this hereditary effect was more important in *Q. alba*. One study by McClennen (1939, cited in Van Dersal 1940) showed regular alternation of good and poor production by one individual of *Q. prinus* over nine years, while an adjacent individual of the same species never produced a good crop.

3.3.2.5.2. Physiology

It has often been suggested that one of the principal reasons for periodic fruiting in oaks is the need to spend several years replenishing the reserves required for a large crop of fruit (e.g., Downs 1949; Evans 1988; Nixon *et al.* 1975; Silvertown 1980; Wood 1938). It is generally acknowledged that masting in trees relates to some extent to this factor, and in fact the energy devoted to flowering/fruiting and to wood production are inter-related to the extent that the effect of heavy seed years can be recognised in annual growth rings of some masting genera (Matthews 1963). Little work has been done on the relative allocation of productivity to reproduction in the oaks, though Rundel (1980) quotes figures ranging from 0.3 to 4.9% of net productivity for six North American species, while suggesting that measurements in years of heavy crops would probably produce larger figures. The causal relations between the size of one year's crop and that of subsequent years are undoubtedly

very complex, but unfortunately very little study has been applied to this area in the oaks. Such influences may be relevant in two major areas:

3.3.2.5.2.1. Effects on flowering

In the case of periodically-flowering species the need to replenish reserves after fruiting is expressed as a failure to flower in the year or years following a mast year. However, in oaks (and some other periodically-fruiting trees) flowers are often produced even in years after heavy crops, and there is no regular alternation of flowering as there is in the cyclically-flowering species of trees. Yearly or frequent flowering has been recorded for many American species, in oaks in Britain, and in the Soviet Union (Jones 1959; Longman and Coutts 1974; Matthews 1963; Shaw 1974). Because of this constancy of flowering in oak trees, and the fact that flowering may occur in quantity even in years of low acorn production, some have considered that variation in flower production was not an important cause of variability in acorn production. Sharp and Sprague (1967), for instance, suggested that a distinction should be made between cyclic flowering and cyclic fruiting species.

It is likely, though, that the crop of acorns produced in any year may influence the laying-down of flower primordia, since growth of the acorns and initiation of the next year's buds take place at the same time. Although flowers may be produced every year the numbers do vary. Feret *et al.* (1982) measured the relation between flower production of individual trees and subsequent acorn production, and they found these to be closely related. They concluded that flower production was of prime importance in controlling whether a tree does or does not produce acorns, and therefore must be of importance in year-to-year variability (though they did not provide any explanation of how the relationship was controlled). Tryon and Carvell (1962) also noted that the numbers of aborted immature acorns found in any year related positively to the number of acorns subsequently produced, which also suggests a significant correlation with original flower number. An experimental study involving grafted clones of *Q. alba* (Farmer 1981) found that there was a significant positive correlation between the abundance of flowers and the subsequent yield over four years.

Sharp and Sprague (1967) found that flowering occurred in every year of their long-term study, where there was marked periodicity of acorn production. They found an abundance of male flowers every year and a varying abundance of, but always some, female flowers. Though female flowers tended to be produced in smaller numbers in the year following that in which the tree had produced abundant acorns, they nevertheless concluded that variation in flower abundance was not the most significant factor in controlling year-to-year variability. They did however comment that many of the female flowers produced were

abnormal in years of subsequent low acorn production, and it may be that this is more important than absolute quantities of flowers produced. Even when there is no numerical relationship then, it is possible that conditions affecting primordia initiation (either related to environmental conditions at the time, or to stresses on the tree's physiology by acorn growth) may be reflected in later flower or fruit abortion, or, conversely, fruiting success.

3.3.2.5.2.2. Effects on acorn growth

Apart from any effect that nutrient demand by acorns in years of heavy cropping might have on flower production, the nutrient budget is almost certainly important in relation to the current production of acorns.

The mechanisms by which the nutrient storage cycle relates to flower primordia initiation and acorn growth has been little studied in oaks however. In one of the Californian evergreen oaks, *Q. agrifolia*, studied by Mooney and Hays (1973), there was no decrease in stored stem carbohydrates as acorns grew, and fruit production apparently depended on currently-produced photosynthates. However this does not exclude the possibility that there is some relationship, since there must be a complex relationship between storage carbohydrates and carbohydrates produced in any one year. The fact that acorn growth is not entirely dependent on currently-produced carbohydrate is supported by observations that in years of severe defoliation of oaks by caterpillars acorn production is not always impeded (Shaw 1974).

3.3.2.5.3. Environment

Variability in environmental factors from year to year may be of importance in periodic fruit production either as favourable factors which induce primordia initiation and flowering, or contribute towards growth conditions in the developing acorn; or as factors which destroy or severely reduce a crop. Environmental factors might have variable effects, so that they might influence only trees of one species, or they might effect all oaks (and perhaps other periodically-fruiting trees), and the area over which the effects might extend could vary enormously. Local environmental differences related to specific site characteristics, or tree position may also have an influence on masting behaviour. Allen and McGinley (1947) found that trees in the open varied in their yearly production more than those growing in stands.

It is possible that climatic factors involved in flowering and fruiting may explain synchronisation of seed production in oak over large parts of Europe as Jensen (1982) suggests appears to be the case for beech masting.

The relationship between year to year environmental variation and acorn production may be complex however. If production does relate to physiological aspects of the tree as discussed in this Appendix, 3.3.2.5.2., and especially if there is a need to build up reserves in years after a heavy crop, then environmental factors such as temperature and precipitation occurring over several years could affect any one year's crop. Few studies have attempted to isolate these long-term effects, though Sharp and Sprague (1967) and Goodrum *et al.* (1971) found no significant relationship between rainfall of the previous year and acorn production, and McQuilkin and Musbach (1977) similarly found no relationship with the current year's precipitation. However, in a study of Kentucky red and white oaks Feldhamer *et al.* (1989) also found no relationship between yield and total precipitation of the previous winter, but there was a significant correlation with the number of days with precipitation in the the previous three and four winters. Neither was there any relationship with cumulative precipitation of the past few years, or the number of days with rain during one or two previous winters, and they suggested that the reason that there was no relation with total precipitation over any particular time scale could be because of the low moisture-holding capacity of the local soils, so that frequency was more important than total amount. Thus any such long-term relationships may well vary between places depending on local factors. Rundel (1980) cites unpublished data of James Griffin indicating a direct relationship between acorn production in *Q. lobata* (a one-year oak) and precipitation during the previous growing season.

3.3.5.2.3.1. Environmental factors favouring acorn production

Certain climatic factors in any one year might be favourable to acorn production at particular stages in the reproductive cycle.

For example, a warm summer is thought to favour the laying down of more flower primordia (Evans 1988; Jones 1959). Wolgast and Stout (1977) found that experimentally high humidity led to the production of significantly higher numbers of flowers (though significantly fewer fertilized acorns were subsequently produced).

Other environmental factors might improve pollination and fertilization success. For example, in their study of the factors affecting acorn production in white oaks Sharp and Sprague (1967) concluded that the most significant effect on variability of production were variations in day and night temperatures in the period of flowering and fruit set, and that a warm period in early spring, followed by a cooler period correlated with years of good acorn production (see this Appendix, 3.2.3.2.1.).

An increase of light to trees may also increase the profusion and regularity of flowering (Matthews 1963), so it is possible that events such as burning, felling, or death of neighbouring trees could increase the regularity of acorn production.

3.3.5.2.3.2. Environmental factors antagonistic to acorn production

Whatever climatic factors might potentially favour flowering and fruiting in oaks in any particular year over different areas, there are other factors which may prevent or diminish flowering or fruit growth, or destroy a crop as it is growing.

The effects of many meteorological factors (frosts, drought, prolonged rainy periods, air temperature, relative humidity, wind movement, precipitation, drought, and vapour pressure) which had previously been noted to apparently adversely affect the intensity of fruiting in masting trees were examined by Sharp and Sprague (1967). They found that the most consistent correlation with years of low yield was a steady increase in temperature from April to May (cf. this Appendix, 3.3.2.5.3.1.) (pollen shedding occurred from mid- to late May). They found no correlation between precipitation, relative humidity, wind velocity, or evaporation rates and subsequent poor acorn production, and concluded that killing frosts in Pennsylvania might account for only four years of total failure and four years of partial failure over a fifty year period.

Many others have, however, particularly noted correlations between killing frosts, especially at or around flowering time, and acorn production. Those who have noted frosts which destroy or drastically reduce crops include Downs (1949), Goodrum *et al.* (1971), Nixon *et al.* (1975), and Wolgast and Trout (1979). The latter found the effects of frost to over-ride any effects attributable to age, stand density, or the application of fertilizer. Baker (1950, cited in Gysel 1956) summarised studies undertaken in Germany, concluding that in some years good crops occur over large areas, while in other years they may be local, largely due to the effects of frost.

Others have examined the effects of less extreme temperature variations. In Britain in cold summers many acorns of *Q. petraea/robur* fail to mature or remain small, and the two oak species apparently have crop failures more often in the north than the south (Jones 1959), probably because of this. Goodrum *et al.* (1971), however found that temperature variations (other than killing frosts) had an inconclusive effect on flowering, fruit set, and yield. Korschgen (1962) has noted reasonable production of acorns in Missouri, when crops of many other species failed due to a drought; and Duncan and Clawson (1980) also recorded heavy fruiting in *Q. douglasii* in a year of drought.

3.3.2.6. Variations in masting between one-year and two-year oaks

Because there are oaks which differ in the time taken between flowering and acorn maturation by one year (see this Appendix, 3.2.4.1., 3.2.5.1.), it is possible that climatic factors that affect some species may not affect those of the other type. Factors which favour flowering should be seen in that year in the one-year oaks, and in the following year in the two-year oaks. A similar pattern might be seen in relation to factors that adversely affect flowering. For example, since the effects of a killing frost are likely to be more extreme at the flowering stage, and less likely to destroy already developing acorns, a frost at flowering time in one year may destroy or diminish fruits in the one-year oaks yet have little effect on the two-year oak crop of that year. A diminishment of the subsequent year's crop would however be expected.

Such a pattern of alternation has been noted in the North American oaks by Goodrum *et al.* (1971) and Nixon *et al.* (1975) in relation to the effects of killing frosts. The latter also noted alternations in years where killing frosts did not occur, suggesting that favourable factors were responsible.

However, extremely severe frost may destroy the immature acorns of red oaks, and Wolgast and Trout (1979) found reduced yields of *Q. ilicifolia* in such a year, where some of the damage resulted from frost-induced mortality of branches with immature acorns. So similar effects of adverse conditions on yields might be noted in both one- and two- year oaks, and a pattern of alternation might not always be the case. Smith and Scarlett (1987) found in Missouri that good crops of red (two-year) and white (one-year) oak acorns coincided rather than alternated over time. This was not apparently correlated with the occurrence of killing frosts, or other obvious effects, and in this case it seems that factors that affected the growth and maturation of the crop were more important than those occurring at flowering time, and that these factors affected all species in the same way.

1.Western North America					
Species	Acorn Weight (g)	% Water (fresh wt)	Shell Wt. (as % of total)	Comments	Source
Erythrobalanus					
Q. agrifolia	2	—	—		Baumhoff 1981
	—	29.1	22	one year	Wolf 1945
	2.3	—	—	1 sample	USDA 1974
Q. kelloggii	3	—	—		"
	3.8 (dry wt)	—	—	bumper crop year	Bowyer & Bleich 1980
	(3.1)-4.8-(8.7) [28]	—	—	49 samples	USDA 1974
		31.4	26-30	max size from exceptional trees	Wolf 1945
Q. wislizenii	2	—	—		Baumhoff 1981
	(3.0)-3.6-(4.5)	—	—	3 samples	USDA 1974
	3.6	29.8	—		Wagnon 1946 (in Passof *et al.* 1985)
	—	—	24/28-30	tree/shrub forms	Wolf 1945
Lepidobalanus					
Q. douglasii	3	—	—		Baumhoff 1981
	1/2 (dry wts)	—	—	low/high producing trees	Graves 1980
	(2.5)-4.5-(8.2)	—	—	4 samples	USDA 1974
	1.9	40.8	—		Wagnon 1946 (in Passof *et al.* 1985)
	6.3	33.6	26	one year	Wolf 1945
Q. dumosa	4.5	—	—	1 samples	USDA 1974
	—	—	24/26	two crops	Wolf 1945
Q. durata	—	—	28	one year	"
Q. garryana	(4.5)-5.3-(6.0)	—	—	3 samples	USDA 1974
	—	30.7	24-26	one year	Wolf 1945
Q. lobata	5	—	—		Baumhoff 1981
	(1.9)-3.5-(6.0)	—	—	4 samples	USDA 1974
	3.5	40.6	—		Wagnon 1946 (in Passof *et al.* 1985)
	—	40.8	22-26		Wolf 1945
Q. turbinella	(1.3)-1.4-(1.5)	—	—	2 samples	USDA 1974
Protobalanus					
Q. chrysolepis	28	42.1	24	maximum; size very variable even on adjacent trees	Wolf 1945
	3.0	—	—	one sample	USDA 1974
Q. dunnii	—	—	42	one year	Wolf 1945
Q. vaccinifolia	(0.3)-0.4-(0.6)	—	—	2 samples	USDA 1974
Lithocarpus densiflorus	—	36	40	one year	Wolf 1945

Table 12. Weight, % moisture, and % shell-weight of acorns (continued over)

2. Eastern North America					
Species	Acorn Weight (g)	% Water (fresh wt)	Shell Wt. (as % of total)	Comments	Source
Erythrobalanus					
Q. arkansana	1.0	—	—		Miller & Lamb 1985
Q. coccinea	2.3 (semi-dry wt)	—	—	Missouri Ozarks	Christisen 1955
	2.3	—	—	large sample area over several yrs; Southern Appalachians	Downs 1944
	(1.1)-1.9-(4.3)	—	—	4 samples	USDA 1974
	1.1-2.9	—	—		Van Dersal 1938
Q. ellipsoidalis	(1.6)-1.9-(2.2)	—	—	11 samples	USDA 1974
Q. falcata	1.4	29	—	mean, 5yrs, 100 trees; Louisisana/East Texas	Goodrum *et al.* 1971
	(0.6)-0.8-(1.4)	—	—	9 samples	USDA 1974
var. *pagodifolia*	(0.6)-0.8-(1.1)	—	—	2 samples	"
Q. ilicifolia	0.6	—	—	1 sample	"
Q. imbricaria	0.6-1.0	—	—		Van Dersal 1938
	(0.6)-1.1-(1.4)	—	—	11 samples	USDA 1974
Q. incana	2.0	31	—	mean, 5yrs, 100 trees; Louisiana/East Texas	Goodrum *et al.* 1971
	1.0	—	—		Miller & Lamb 1985
Q. laevis	1.1	—	—	1 samples	USDA 1974
Q. laurifolia	(0.7)-0.8-(1.2)	—	—	3 samples	"
	0.7-0.8	—	—		Van Dersal 1938
Q. marilandica	1.1/1.3 (semi-dry wt)	—	—	two locations; Missouri Ozarks	Christisen 1955
	2.0 (1.6)	33	—	fresh wt (dry weight) means, 5yrs, 100 trees; Louisiana/East Texas	Goodrum *et al.* 1971
Q. nigra	0.7 (dry wt)	—	—	Mississippi bottomlands	Delnicki & Reinecke 1986
	1.4	30	—	mean, 5yrs, 120 trees; Louisiana/East Texas	Goodrum *et al.* 1971
	(0.6)-1.1-(2.0)	—	—	15 samples	USDA 1974
	0.8-1.1	—	—		Van Dersal 1938
Q. nuttallii	2.6 (dry wt)	—	—	Mississippi bottomlands	Delnicki & Reinecke 1986
	(3.2)-4.8-(8.1)	—	—	11 samples	USDA 1974
Q. palustris	6.4	33	33	one yr; France (introduced)	Gaussen & Rouquette 1949
	1.1	—	—		McQuilkin & Musbach 1977
	(0.8)-1.1-(1.4)	—	—	3 samples	USDA 1974
	0.8	—	—		Van Dersal 1938

Table 12. Weight, % moisture, and % shell-weight of acorns (cont.)

Species	Acorn Weight (g)	% Water (fresh wt)	Shell Wt. (as % of total)	Comments	Source
Q. phellos	0.6 (dry wt)	—	—	Mississippi bottomlands	Delnicki & Reinecke 1986
	1.1	31	—	mean, 5yrs, 100 trees; Louisiana/East Texas	Goodrum *et al.* 1971
	—	—	30.1		King and McClure 1944
	(0.7)-1.0-(1.7)	—	—	14 samples	USDA 1974
	0.8	—	—		Van Dersal 1938
Q. pumila	0.8	—	—		Miller & Lamb 1985
Q. rubra	5.0	—	—	large sample area over several yrs; Southern Appalachians	Downs 1944
	(5.5)-6.2-(7.0)	23	33	range and mean, two yrs, several areas; France (introduced)	Gaussen & Rouquette 1949
	4.6	—	—	mean 5 yrs, 15 trees, sound acorns	Gysel 1957
	3.0 (dry wt)	—	—	kernel only; Illinois	Havera & Smith 1979
	(2.5)-5.3-(8.0)	[33.3-37.5]	—	range and mean of 184 acorns of one yr; North Carolina	Korstian 1927
	3.4	37.8	—	kernel only, mean of 35 post-winter acorns; New York	Lewis 1982
	4.6 (dry wt)	—	53 (of dry wt)	mean from one tree; Missouri	Smith & Follmer 1972
	(1.8)-3.6-(6.0)	—	—	33 samples	USDA 1974
	4.5-5.7	—	—		Van Dersal 1938
Q. shumardii	3.2 (dry wt)	—	27 (of dry wt)	mean from one tree; Missouri	Smith & Follmer 1972
	(3.5)-4.5-(5.8)	—	—	3 samples	USDA 1974
Q. velutina	1.9/1.6 (semi-dry wt)	—	—	two locations; Missouri Ozarks	Christisen 1955
	1.9	—	—	large sample area over several yrs; Southern Appalachians	Downs 1944
	1.4	—	—	mean 5 yrs, 15 trees, sound acorns	Gysel 1957
	1.2 (dry wt)	—	—	kernel only; Illinois	Havera & Smith 1979
	(0.3)-1.9-(2.8)	[33.3-37.5]	—	range and mean of 232 acorns of one yr; North Carolina	Korstian 1927
	(1.1)-1.9-(3.6)	—	—	7 samples	USDA 1974
	1.5-3.5	—	—		Van Dersal 1938

Table 12. Weight, % moisture, and % shell-weight of acorns (cont.)

Species	Acorn Weight (g)	% Water (fresh wt)	Shell Wt. (as % of total)	Comments	Source
Lepidobalanus					
Q. alba	2.7/4.4 (semi-dry wt)	—	—	two locations; Missouri Ozarks	Christisen 1955
	2.7	—	—	large sample area over several yrs; Southern Appalachians	Downs 1944
	4.4	50	—	mean, 5yrs, 100 trees; Louisiana/East Texas	Goodrum *et al.* 1971
	1.8-3.2	—	—	range good and poor sites and years, 5 yrs, 15 trees, sound acorns	Gysel 1957
	3.3 (dry wt)	—	—	kernel only; Illinois	Havera & Smith 1979
	4.3	—	—	mean, 2 yrs, one good, one poor production; Central Illinois	Johnson 1975
	(0.5)-2.7-(6.0)	[37.5-41.2]	—	range and mean of 409 acorns of one yr; North Carolina	Korstian 1927
	1.4	42.4	—	kernel only, mean of 144 post-winter acorns; New York	Lewis 1982
	0.8 (dry wt)	—	50 (of dry wt)	mean from one tree; Missouri	Smith & Follmer 1972
	(2.2)-3.8-(6.5)	—	—	23 samples	USDA 1974
	3.0-4.5	—	—		Van Dersal 1938
Q. bicolor	3.6-5.0	—	—		"
	(2.6)-3.8-(5.0)	—	—	3 samples	USDA 1974
Q. durandii	1.6	—	—	one sample	"
Q. lyrata	4.1	46	—	mean, 5yrs, 100 trees; Louisiana/East Texas	Goodrum *et al.* 1971
	(3.0)-3.2-(3.5)	—	—	4 samples	USDA 1974
	3.0	—	—		Van Dersal 1938
Q. macrocarpa	7.7 (dry wt)	—	—	kernel only; Illinois	Havera & Smith 1979
	6.7 (dry wt)	—	30 (of dry wt)	mean from one tree; Missouri	Smith & Follmer 1972
	(3.4)-6.0-(11.3)	—	—	8 samples	USDA 1974
	1.1-1.2	—	—		Van Dersal 1938
Q. michauxii	9.7	52	—	5yrs, 80 trees; Louisiana/East Texas	Goodrum *et al.* 1971
	(2.3)-5.3-(13.0)	—	—	9 samples	USDA 1974
	3.0-6.5	—	—		Van Dersal 1938
Q. muehlenbergii	(0.9)-1.1-(1.7)	—	—	4 samples	USDA 1974
	0.9	—	—		Van Dersal 1938
Q. prinoides	1.1	—	—		"

Table 12. Weight, % moisture, and % shell-weight of acorns (cont.)

Species	Acorn Weight (g)	% Water (fresh wt)	Shell Wt. (as % of total)	Comments	Source
Q. prinus	6.6	—	—	large sample area over several yrs; Southern Appalachians	Downs 1944
	(0.5)-5.1-(12.5)	[37.5-41.2]	—	range and mean of 210 acorns of one yr; North Carolina	Korstian 1927
	2.3	46.5	—	kernel only, mean of 215 post-winter acorns; New York	Lewis 1982
	(2.3)-4.5-(8.3)	—	—	5 samples	USDA 1974
	3.0-7.6	—	—		Van Dersal 1938
Q. stellata	1.1	—	—	immature acorns, August	Christisen 1951
	1.0 (semi-dry wt)	—	—	Missouri Ozarks	Christisen 1955
	2.1	39	—	5yrs, 100 trees; Louisiana/East Texas	Goodrum *et al.* 1971
	(0.7)-1.2-(2.3)	—	—	9 samples	USDA 1974
	0.7-9.2	—	—		Van Dersal 1938
Q. virginiana	1.6	42	—	5yrs, 100 trees; Louisiana/East Texas	Goodrum *et al.* 1971
	(0.9)-1.3-(1.9)	—	—	4 samples	USDA 1974
3. Europe and the Mediterranean					
Q. cerris	4.0	39.5	22.5	mean wt one yr, Italy	Petrucci 1947
	8.1	42.4	22.2	"	"
	6.0	41.0	22.4	mean wt two yrs, Italy	"
	(3.1)-4.1-(7.6)	—	—	4 samples	USDA 1974
	(1.7)-2.7-(3.6)	—	—	range and mean, 9 acorns, S. England (introduced)	Watt 1919
Q. coccifera	(2.2)-2.8-(3.8)	34	23	range and mean, one yr, several areas; France	Gaussen & Rouquette 1949
Q. ilex	—	(26.6)-29.1-(32.3)	(18.0)-18.7-(20.0)	range and mean, samples from 8 locations; Spain	Mazuelos Vela *et al.* 1961
	(1.6)-2.3-(3.0)	33	17	range and mean, one yr, several areas; France	Gaussen & Rouquette 1949
	2.0	40.4	16.3	mean wt one yr, Italy	Petrucci 1947
	3.3	40.3	16.7	"	"
	2.7	40.3	16.5	mean wt two yrs, Italy	"
Q. petraea	0.1-6.0	—	—		Brookes & Wigston 1979
	(3.0)-5.1-(6.5)	41	18	range and mean,one yr, several areas; France	Gaussen & Rouquette 1949
	(1.2)-2.5-(7.0)	c.50%	—	range and mean; Oxford area, UK	Jones 1959
	2.9-3.7	—	—	means of various studies; continent	"
	2.4	44.8	17.8	mean wt one yr, Italy	Petrucci 1947
	2.7	38	18.5	"	"
	2.5	41.4	18.1	mean wt two yrs, Italy	"
	2.3	—	—		Salisbury 1942
	(1.5)-2.7-(7.6)	—	—	9 samples	USDA 1974
Q. pubescens	(1.4)-4.2-(7.1)	33	23	range and mean, one yr, several areas; France	Gaussen & Rouquette 1949
Q. pyrenaica	(3.4)-4.1-(5.3)	41	18	range and mean, one yr, two areas; France	"

Table 12. Weight, % moisture, and % shell-weight of acorns (cont.)

Species	Acorn Weight (g)	% Water (fresh wt)	Shell Wt. (as % of total)	Comments	Source
Q. robur	0.1-4.5	—	—	good crop of normal-sized acorns	Brookes & Wigston 1979
	2.5-12	—	—	previous site, following year; good crop with some v. large acorns	"
	(3.7)-4.8-(5.5)	36	19	range and mean, one yr, several areas; France	Gaussen & Rouquette 1949
	(1.6)-3.5-(8.8)	c.50%	—	range and mean; Oxford area, UK	Jones 1959
	4.0-4.7	—	—	means of various studies; continent	"
	4.3	33.1	15.5	mean wt one yr, Italy	Petrucci 1947
	4.5	33.5	19.1	"	"
	6.2	40.4	18.8	one tree with exceptionally large acorns, Italy	"
	4.4	33.3	17.3	mean wt two yrs, Italy	"
	3.9	—	—		Salisbury 1942
	(2.0)-3.5-(5.0)	—	—	10 samples	USDA 1974
Q. suber	4.6	35	17	mean, one yr, several areas; France	Gaussen & Rouquette 1949
	(4.5)-6.0-(9.1)	—	—	13 samples	USDA 1974
Q. petraea/robur	(5.5)-7.1-(9.9)	—	—	range and mean 38 acorns, S. England	Watt 1919
	—	60	—		Guppy 1912 (in Watt 1919)
Q. sp.	—	—	22.3	Lebanon	Kuzayli et al. 1966
4. Eastern Asia					
Cyclo-balanopsis					
Q. argentata	4.9 (dry wt)	—	—	mean of 5 largest specimens; W. Malaysia, at 600m	Kaul 1985
Q. austro-cochinchinensis	1.5 (dry wt)	—	—	mean of 5 largest specimens; Thailand, at 1270m	"
Q. cambodiensis	3.9 (dry wt)	—	—	mean of 5 largest specimens; Cambodia, at 1000m	"
Q. championii	0.9 (dry wt)	—	—	mean of 5 largest specimens; Taiwan, at 300m	"
Q. elmeri	5.8 (dry wt)	—	—	mean of 5 largest specimens; Borneo, at 695m	"
Q. gemelliflora	2.6 (dry wt)	—	—	mean of 5 largest specimens; Borneo, at 1600m	"
Q. glauca	0.3 (dry wt)	—	—	mean of 5 largest specimens; Burma, at 1050m	"
Q. kerangasensis	1.7 (dry wt)	—	—	mean of 5 largest specimens; Borneo, at 2m	"
Q. lamellosa	2.6 (dry wt)	—	—	mean of 5 largest specimens; India, at 2500m	"
Q. leuco-trichophora	0.9 (dry wt)	—	—	mean of 5 largest specimens; India, at 1600m	"
Q. mespilifolioides	0.7 (dry wt)	—	—	mean of 5 largest specimens; Thailand, at 1410m	"
Q. morii	0.1 (dry wt)	—	—	mean of 5 largest specimens; Taiwan, at 2300m	"

Table 12. Weight, % moisture, and % shell-weight of acorns (cont.)

Species	Acorn Weight (g)	% Water (fresh wt)	Shell Wt. (as % of total)	Comments	Source
Q. oidocarpa	4.6 (dry wt)	—	—	mean of 5 largest specimens; W. Malaysia, at 1600m	Kaul 1985
Q. pachyloma	3.3 (dry wt)	—	—	mean of 5 largest specimens; Taiwan, at 200m	"
Q. saravanensis	1.4 (dry wt)	—	—	mean of 5 largest specimens; Thailand, at 1700m	"
Q. stenophylloides	0.1 (dry wt)	—	—	mean of 5 largest specimens; Taiwan, at 1500m	"
Q. subsericea	1.4 (dry wt)	—	—	mean of 5 largest specimens; Borneo, at 1450m	"
Q. valdinervosa	5.7 (dry wt)	—	—	mean of 5 largest specimens; Borneo, at 2100m	"
Quercus					
Q. acutissima	(4.1)-4.5-(4.8)	—	—	2 samples; grown in North America	USDA 1974
Q. dealbata	0.3-1.3	—	—	sub-tropical wet hill forest; NE India	Tripathi & Khan 1990
Q. floribunda	2.7 (dry wt)	—	—	mean of 5 largest specimens; India, at 1900m	Kaul 1985
Q. griffithii	0.2-1.1 0.2 (dry wt)	— —	— —	sub-tropical wet hill forest; NE India mean of 5 largest specimens; Burma, at 1050m	Tripathi & Khan 1990 Kaul 1985
Q. ilex	—	—	28.8	dry oak scrub; Pakistan	Khan *et al.* 1977
Q. lanata	0.1 (dry wt)	—	—	mean of 5 largest specimens; India, at 2100m	Kaul 1985
Q. serrata	0.5 (dry wt)	—	—	mean of 5 largest specimens; Burma, at 1050m	"
Q. setulosa	0.1 (dry wt)	—	—	mean of 5 largest specimens; Vietnam, at 700m	"
Q. variabilis	(3.7)-4.4-(6.1)	—	—	12 samples	USDA 1974

Table 12. Weight, % moisture, and % shell-weight of acorns (concluded)

1.Western North America				
Species	Yield (kg/tree)	Frequency of Good Crop	Comments	Source
Erythrobalanus				
Q. agrifolia	<45 2	1 in 2 yrs —	 good year	Baumhoff 1963 Baumhoff 1981
Q. emoryi	70 litres 140 litres 23/45 (5)-15-(27) acorns/tree	— some nearly every yr some nearly every yr —	one tree good trees poor and maximum yrs mean and ranges from three different oak woodland types; Arizona	Smith 1929 " " Trail 1980
Q. hypoleucoides	3 acorns/tree	—	mean from pine-oak woodland; Arizona	"
Q. kelloggii	90-135 6 4.5/27.2 — 102 9-45-(90-130) — — — 73	>1 in 2 yrs — — 1 in 2/3 yrs 2 in 3, partial every yr — 1 in 5/6 yrs 1 in 2-3 yrs more regular than many other spp —	good year yield good year means for 110 trees, <80yr old/40cm DBH and > 80 yr old/40-96cm DBH trees, central California production often low in other yrs maximum production; Shasta Forest average and maximum ranges young-growth stands, crops excellent or non-existent acorns produced abundantly average tree with heavy crop	Baumhoff 1963 Baumhoff 1981 Graves 1977 (in Potter & Johnston 1980) Roy 1962 (in Potter & Johnston 1980) Smith 1929 " Tappeiner & McDonald 1980 USDA 1974 Wolf 1945
Q. wislizenii	2 70 litres — —	— 1 in 2 yrs 1 in 5-7 yrs —	good year based on 12 trees not produced in very great quantities	Baumhoff 1981 Smith 1929 USDA 1974 Van Dersal 1938
Lepidobalanus				
Q. arizonica	(7)-17-(30) acorns/tree	—	mean and ranges from three different oak woodland types; Arizona	Trail 1980
Q. douglasii	6 — — 73	1 in 3 yrs — 1 in 2-3 yrs — —	good year acorns produced abundantly average tree with heavy crop	Baumhoff 1963 Baumhoff 1981 USDA 1974 Van Dersal 1938 Wolf 1945
Q. dumosa	— —	— —	acorns not plentiful crop usually ight and very uncertain	Baumhoff 1963 Van Dersal 1938
Q. garryana	230/270 70 litres — 23 4.5-9/9-18	1 in 3/4 yrs — 1 in 2-3 yrs — —	good trees, one yr one small tree one tree fair/good years, av several trees	Smith 1929 " USDA 1974 Wolf 1945 "

Table 13. Yields of acorn recorded/tree (continued over)

Species	Yield (kg/tree)	Frequency of Good Crop	Comments	Source
Q. lobata	25	—	good year	Baumhoff 1981
	(7)-34-(74) acorns/m^2 crown	—	ranges and mean, density beneath trees, 4 trees over 9 yrs, viable acorns	Griffin 1980a
	(0)-74-(207) acorns/m^2 crown	Failed 2 of 9 yrs	ranges and mean, density beneath tree, 1 "productive" tree over 9 yrs	"
	80	1 in 3 yrs, partial crop 2 of 3 yrs	maximum crop	Smith 1929
	27-54	1/2 of 3 yrs	good yrs	"
	—	1 in 2-3 yrs		USDA 1974
	>225	—	isolated tree, small acorns (trees with larger acorns perhaps twice this amount)	Wolf 1945
Protobalanus				
Q. chrysolepis	68-225	1 in 3 yrs		Baumhoff 1963
	180	—	one exceptional tree, one yr	Wolf 1945
Quercus sp.	73-450/905	—	12,000 - 150,000 acorns/tree, year of bumper crop	Baumhoff 1981
Lithocarpus densiflorus	14-136	irregular, partial crop every yr	good year, range dependent on tree size and situation	Smith 1929
	88 litres	—	average production	"
	>90	—	crop size varies, some every year	Baumhoff 1963
2. Eastern North America				
Erythrobalanus				
Q. coccinea	(0)-1.2-(5.3)	1 of 5 yrs	5-yr mean and ranges, based on semi-dried wt; Missouri Ozarks	Christisen 1955
	0.2-(3.1)	—	sound acorns only, based on semi-dried wt, mean and max, 6-yrs; Missouri Ozarks	"
	9.9 acorns/m^2 crown	—	good yr, 48 samples; Southcentral Missouri	Dalke 1953
	(1.1)-5.3-(8.0)	[2 of 7 yrs]	7-yr mean and ranges for trees of 10 size classes; Southern Appalachians	Downs 1944 [" & McQuilkin 1944]
	105.8	—	one year, exceptional tree (others a fraction of this number)	Downs 1949
	—	1 in 3-5 yrs		USDA 1974
Q. falcata	(0.02)-1.6-(7.6)	—	range and mean, 18 yrs, large site; Louisisana/E. Texas	Goodrum *et al.* 1971
	0.6 litres (1.6 l)	—	4-yr mean and range; W. Virginia	Park 1942
	—	1 in 1-2 yrs		USDA 1974
Q. imbricaria	—	1 in 2-4 yrs		"
Q. incana	(0.3)-1.2-(1.9)	—	range and mean, 6 yrs, large site; Louisisana/E. Texas	Goodrum *et al.* 1971
	0.8	annual ?	15cm d.b.h. tree, "each year"	Miller & Lamb 1985
	—	—	"fruit produced in great profusion"	Van Dersal 1938
Q. laurifolia	—	annual		USDA 1974

Table 13. Yields of acorn recorded/tree (cont.)

Species	Yield (kg/tree)	Frequency of Good Crop	Comments	Source
Q. marilandica	(0.2)-0.8-(1.8)	3 of 6 yrs	6-yr mean and ranges, based on semi-dried wt; Missouri Ozarks	Christisen 1955
	0.1-(0.2)	—	sound acorns only, based on semi-dried wt, mean and max, 6-yrs; Missouri Ozarks	"
	1.8/0.4 acorns/m^2 crown	—	two consecutive yrs; Southcentral Missouri	Dalke 1953
	(0.08)-0.3-(1.1)	—	range and mean, 18 yrs, large site; Louisisana/E. Texas	Goodrum *et al.* 1971
	—	almost annual		Miller & Lamb 1985
	0.01 litres (0.01 l)	—	4-yr mean and range; W. Virginia	Park 1942
Q. nigra	(274)-3384-(8720) acorns/tree	—	ranges and mean,15 trees, 1938	Cypert & Webster 1948
	(869)-11500-(93000) acorns/tree	—	ranges and mean, 15 trees, 1939	"
	(96)-9039-(28360) acorns/tree	—	ranges and mean, 15 trees, 1940	"
	(0.4)-3.2-(5.6)	—	range and mean, 6 yrs, large site; Louisisana/E. Texas	Goodrum *et al.* 1971
	—	1 in 1-2 yrs		USDA 1974
Q. nuttallii	—	1 in 3-4 yrs		"
Q. palustris	—	2/3 of 4 yrs medium; 1 of 3/4 poor; 1 in 12 yrs excellent	12 yr study; SE Missouri	McQuilkin & Musbach 1977
	—	1 in 1-2 yrs		USDA 1974
Q. phellos	(95)-3312-(9450) acorns/tree	—	ranges and mean, 15 trees, 1938	Cypert& Webster 1948
	(622)-10999-(52220) acorns/tree	—	ranges and mean, 15 trees, 1939	"
	(0)-5357-(10350) acorns/tree	—	ranges and mean, 15 trees, 1940	"
	—	annual		USDA 1974

Table 13. Yields of acorn recorded/tree (cont.)

Species	Yield (kg/tree)	Frequency of Good Crop	Comments	Source
Q. rubra	6.4/3.6 acorns/m^2 crown	—	two consecutive yrs; Southcentral Missouri	Dalke 1953
	(0.2)-4.4-(7.8)	[2 of 7 yrs]	7-yr mean and ranges for trees of 14 size classes; Southern Appalachians	Downs 1944 [" & McQuilkin 1944]
	108	—	one tree	Korstian 1927
	50.9	—	50cm d.b.h. trees on good sites	Miller & Lamb 1985
	0.5 litres (0.5 l)	—	4-yr mean and range; W. Virginia	Park 1942
	(99)-837-(3535) acorns/tree	—	mature acorns, range and mean 9 trees, one year; oak-hickory forest, Missouri	Sork 1984
	(c.3)-41.9-(c.86) acorns/m^2 crown	—	mature acorns, range and mean over 5 yrs of 14 individual trees; West Virginia	Tryon & Carvell 1962
	(c.19)-42.0-(c.81.5) acorns/m^2 crown	—	mature acorns, average annual production of all 14 trees over 5 yrs; West Virginia	"
	—	1 in 3-5 yrs		USDA 1974
Q. shumardii	—	1 in 2-3 yrs		"
Q. velutina	(0.4)-1.6-(4.0)	2 of 6 yrs	6-yr mean and ranges, based on semi-dried wt; Missouri Ozarks	Christisen 1955
	0.3-(1.5)	—	sound acorns only, based on semi-dried wt, mean and max, 6-yrs; Missouri Ozarks	"
	5.3/1.1 acorns/m^2 crown	—	two consecutive yrs; Southcentral Missouri	Dalke 1953
	(0.5)-2.3-(4.0)	[2/3 of 7 yrs]	7-yr mean and ranges for trees of 14 size classes; Southern Appalachians	Downs 1944 [" & McQuilkin 1944]
	(3.2)-32.3-(72)g/m^2 crown	2 of 8 yrs (4 medium, 2 low)	ranges and mean, 8 yrs, 15 trees; Michigan	Gysel & Lemmien 1964
	9.4	—	mean, 9 trees, one yr, all acorns, North Carolina	Korstian 1927
	0.5 litres (0.5l)	—	4-yr mean and range; W. Virginia	Park 1942
	—	1 in 2-3 yrs		USDA 1974

Table 13. Yields of acorn recorded/tree (cont.)

Species	Yield (kg/tree)	Frequency of Good Crop	Comments	Source
Lepidobalanus				
Q. alba	(1.8)-4.0-(6.8)	2 of 6 yrs	6-yr mean and ranges, based on semi-dried wt; Missouri Ozarks	Christisen 1955
	0.5-(1.3)	—	sound acorns only, based on semi-dried wt, mean and max, 6-yrs; Missouri Ozarks	"
	1.6/2.4 acorns/m^2 crown	—	two consecutive yrs; Southcentral Missouri	Dalke 1953
	(0.3)-3.8-(5.9)	[3 of 7 yrs]	7-yr mean and ranges for trees of 14 size classes; Southern Appalachians	Downs 1944 [" & McQuilkin 1944]
	248/16416 acorns/tree	—	mean, 4 trees, two bad crop years/two good crop years; Virginia	Feret *et al.* 1982
	(0.3)-3.2-(5.1)	—	range and mean, 5 yrs, large site; Louisisana/E. Texas	Goodrum *et al.* 1971
	38	—	one tree, North Carolina	Korstian 1927
	13.3	—	mean, 12 trees, one yr, all acorns, North Carolina	"
	1.1 litres (2.2 l)	—	4-yr mean and range; W. Virginia	Park 1942
	(c. 4)-23.7-(c.74) acorns/m^2 crown	—	mature acorns, range and mean over 5 yrs of 14 individual trees; West Virginia	Tryon & Carvell 1962
	(c. 11.1)-23.7-(c. 42.0) acorns/m^2 crown	—	mature acorns, average annual production of all 14 trees over 5 yrs; West Virginia	"
	—	1 in 4-10 yrs		USDA 1974
	—	1 in 8/10 yrs	"full crop", some seed almost every yr	Van Dersal 1938
Q. lyrata	—	1 in 3/4 yrs		"; USDA 1974
Q. macrocarpa	—	1 in 2-3 yrs		USDA 1974
Q. michauxii	(0.5)-2.5-(3.7)	—	range and mean, 4 yrs, large site; Louisisana/E. Texas	Goodrum *et al.* 1971
	—	1 in 3-5 yrs		USDA 1974
Q. prinus	(0.4)-3.8-(5.0)	[2/3 of 7 yrs]	7-yr mean and ranges for trees of 14 size classes; Southern Appalachians	Downs 1944 [" & McQuilkin 1944]
	8.9	—	mean, 15 trees, one yr, all acorns, North Carolina	Korstian 1927
	(34)-641-(2010) acorns/tree	1 in 2 yrs	range and mean 10 yrs, one tree	McClennen 1939 (in Van Dersal 1940)
	(0)-39-(282) acorns/tree	1 medium yr in 10	range and mean 10 yrs, adjacent tree	"
	1.4 litres (2.8 l)	—	4-yr mean and range; W. Virginia	Park 1942
	—	1 in 2-3 yrs		USDA 1974

Table 13. Yields of acorn recorded/tree (cont.)

Species	Yield (kg/tree)	Frequency of Good Crop	Comments	Source
Q. stellata	2.6	—	one tree, immature acorns, August	Christisen 1951
	(0.2)-0.2-(0.3)	v similar over 6 yrs	6-yr mean and ranges, based on semi-dried wt; Missouri Ozarks	Christisen 1955
	0.01-(0.05)	—	sound acorns only, based on semi-dried wt, mean and max, 6-yrs; Missouri Ozarks	"
	2.1/3.4 acorns/m^2 crown	—	two consecutive yrs; Southcentral Missouri	Dalke 1953
	(0.03)-1.4-(4.4)	—	range and mean, 18 yrs, large site; Louisisana/E. Texas	Goodrum *et al.* 1971
	—	1 in 2-3 yrs		USDA 1974
	—	1 in 2/3 yrs		Van Dersal 1938
Q. turbinella	—	1 in 3-5 yrs		USDA 1974
Q. virginiana	—	annual		"
Q. alba, *Q. prinus* and *Q. prinoides*	—	5 of 14 yrs; 8 of 14 poor; 1 failure	14 yr study; Pennsylvania, similar production across Ohio, Indiana, Illinois, Iowa and Nebraska	Sharp & Sprague 1967
Q. spp	—	1 in 3/4 yrs	average of *Q. alba*, *Q. coccinea*, *Q. prinus*, *Q. rubra* and *Q. velutina*	Downs 1949
Q. spp	—	1 in < 5 yrs	average of *Q. alba*, *Q. coccinea*, *Q. marilandica*, *Q. stellata*, and *Q. velutina*	Burns *et al.* 1954
3. Europe and the Mediterranean				
Q. cerris	—	1 in 5-6 yrs	northern Hungary	Juhász & Jakucs 1985
Q. ilex	12-18	annual	some heavy producers, others almost sterile; Sierra Morena, SW Spain	Parsons 1962
	400/600	—	2 exceptional trees, Portugal/Spain	"
	7.6-40	—	production of individual trees variable	Mazuelos Vela *et al.* 1961
	240/1200 litres	1 in 2 yrs	1 tree, repeated alternate yrs; Algarve, Portugal	Smith 1929
	100-400	1 in 2 yrs (area as a whole constant production)	numerous individuals, dehesa; Portugal	"
	350/20-50	1 in 2 yrs	repeated good and poor yrs; Corsica	"
Q. faginea	less abundant than *Q. ilex*	1 in 2 yrs	SW Spain	Parsons 1962
Q. petraea	—	2-5yrs		Evans 1988
	16.3	—	from 120-140 yr old stands, good yr; Oxford	Jones 1959
	844 acorns/m^2 crown	—	small-seeded prolific tree; Oxford	"
	—	1 in 5-6 yrs	northern Hungary	Juhász & Jakucs 1985
	—	1 in 5-7 yrs		USDA 1974
	100 acorns/m^2 crown	—	300-yr old trees, good yr; Germany	Vanselow 1949 (in Jones 1959)
	20000-21000 acorns	—	500-600 yr old standards, good yr; Germany	"

Table 13. Yields of acorn recorded/tree (cont.)

Species	Yield (kg/tree)	Frequency of Good Crop	Comments	Source
Q. robur	—	3-6yrs		Evans 1988
	24.5	—	from 120-140 yr old stands, good yr; Oxford	Jones 1959
	—	1 in 2-4 yrs		USDA 1974
Q. suber	less abundant than *Q. ilex*	highly erratic; no more than 1 in 2 yrs	SW Spain	Parsons 1962
	840 litres	probably 1 in 2 yrs	estate managed for cork; Portugal	Smith 1929
	—	1 in 2-4 yrs		USDA 1974
Q. petraea/robur	—	1 in 6/7yrs; moderate crops 1 in 3/4 yrs	+ frequent yrs of failure (may be pockets of abundant crops in poor yrs and v.v.); all for widespread area of S. England	Jones 1959
	—	1 in 3/4 - 1 in 8/10	heavy crops, favourable/unfavourable areas, France (some districts 20-25 yrs with little crop)	"
4. Eastern Asia				
Q. acutissima	—	annual		USDA 1974
Q. variabilis	—	1 in 2 yrs		"

Table 13. Yields of acorn recorded/tree (concluded)

1.Western North America			
Species	Yield (kg/ha)	Comments	Source
Erythrobalanus			
Q. agrifolia	200	good seed year; N. Coast Ranges, California	Baumhoff 1981
	1568	one yr, 65 ha tract, very large trees covering 40-50%	Wolf 1945
Q. kelloggii	5200	good yr; Sierra Nevada, California	Bainbridge 1987
	600	good seed year; N. Coast Ranges, California	Baumhoff 1981
	1175	largest crop in memory; montane S. California	Bowyer & Bleich 1980
	0-1727 (dry wt)	ranges of several stands, several yrs; central California	Graves 1976 (in Verner 1980)
	616/36	two consecutive yrs, for ha of tree canopy; oak savannah; N. Coast Ranges, California	Menke & Fry 1980
Q. wislizenii	200	good seed year; N. Coast Ranges, California	Baumhoff 1981
	0-109 (dry wt)	ranges of several stands, several yrs; central California	Graves 1976 (in Verner 1980)
	1074/614	two consecutive yrs, for ha of tree canopy; oak savannah; N. Coast Ranges, California	Menke & Fry 1980
Lepidobalanus			
Q. douglasii	600	good seed year; N. Coast Ranges, California	Baumhoff 1981
	10.1-214 (dry wt)	ranges of several stands, several yrs; central California	Graves 1976 (in Verner 1980)
	2955/88	two consecutive yrs, for ha of tree canopy; oak savannah; N. Coast Ranges, California	Menke & Fry 1980
	5600	good season, stands with 50% tree cover	Wolf 1945
	180	good season, areas with 2.5 trees/ha	"
Q. garryana	225/450	fair/heavy years,typical stand, 60 trees/ha	Wolf 1945
Q. lobata	1000	good seed year; N. Coast Ranges, California	Baumhoff 1981
Protobalanus			
Q. chrysolepis	5200	good yr; Southern California	Bainbridge 1987
	2195 (dry wt)	one stand; central California	Graves 1976 (in Verner 1980)
	c. half *Q. kelloggii*	estimated average	Wolf 1945
Lithocarpus densiflorus	c. same as *Q. kelloggii*	estimated average	Wolf 1945
2. Eastern North America			
Erythrobalanus			
Q. coccinea	29.2	large sample from one year, incs undeveloped/wormy acorns; oak-hickory forest, Missouri	Dalke 1953
	24.8/23.6	calculated from 7 yrs crops, from normal/exceptionally mature stands; Southern Appalachians	Downs 1944
Q. imbricaria	(0)-0.3-(0.8)	ranges and mean 3 yrs study; oak-hickory forest, upland sites, E-C Illinois	Havera & Nixon 1980
Q. marilandica	14.6/2.2	large sample, two consecutive years, incs undeveloped/wormy acorns; oak-hickory forest, Missouri	Dalke 1953

Table 14. Yield of acorns/unit area - individual species (continued over)

Species	Yield (kg/ha)	Comments	Source
Q. palustris	392.4	mean of 12 yrs, total acorns inc undeveloped and wormy, some *Q. phellos* inc in count; bottomlands, SE Missouri	McQuilkin & Musbach 1977
	231.2	as previous fully-developed acorns only, inc wormy	"
	171.5	as previous fully-developed sound acorns only	"
	(9.0)-(110.0-275.0)-(489.5)	min and max + range of medium annual production over 12 yrs, fully-developed sound acorns only	"
	(13.6)-176.5-(461.7)	ranges and mean, 5 yrs; bottomlands SE Missouri	Merz & Brakhage 1964
Q. pumila	0.2-2.4	ranges in slash pine plantations from 2-10yrs old; coastal flatwoods, Georgia	Johnson & Landers 1978
	2.5/0.01	2 yrs and 4 yrs after burning; coastal flatwoods, Georgia	"
Q. rubra	255.4/40.3	large sample, two consecutive years, incs undeveloped/wormy acorns; oak-hickory forest, Missouri	Dalke 1953
	19.8/24.8	calculated from 7 yrs crops, from normal/exceptionally mature stands; Southern Appalachians	Downs 1944
	350.6	mean 5 yrs, 15 trees, well-developed acorns	Gysel 1957
	161.3	mean 5 yrs, 15 trees, sound acorns only	"
	(0)-25.3-(61.9)	ranges and mean 3 yrs study; oak-hickory forest, upland sites, E-C Illinois	Havera & Nixon 1980
	(0)-124.2-(255.4)	ranges and mean 3 yrs study; oak-hickory forest, ravine sites, E-C Illinois	"
	23.8	kernel wt. only, one yr study, mixed second-growth hardwood and conifer; New York	Lewis 1982
Q. velutina	61.6/6.7	large sample, two consecutive years, incs undeveloped/wormy acorns; oak-hickory forest, Missouri	Dalke 1953
	9.1/11.1	calculated from 7 yrs crops, from normal/exceptionally mature stands; Southern Appalachians	Downs 1944
	192.6/224.0	poor/medium sites, mean 5 yrs, 15 trees, well-developed acorns	Gysel 1957
	44.8/118.7	poor/medium sites, mean 5 yrs, 15 trees, sound acorns only	"
	(10.0)-204.3-(491.1)	ranges and mean 3 yrs study; oak-hickory forest, upland sites, E-C Illinois	Havera & Nixon 1980
	(1.6)-78.5-(204.1)	ranges and mean 3 yrs study; oak-hickory forest, ravine sites, E-C Illinois	"

Table 14. Yield of acorns/unit area - individual species (cont.)

Species	Yield (kg/ha)	Comments	Source
Lepidobalanus			
Q. alba	23.5/24.6	large sample, two consecutive years, incs undeveloped/wormy acorns; oak-hickory forest, Missouri	Dalke 1953
	17.6/20.9	calculated from 7 yrs crops, from normal/exceptionally mature stands; Southern Appalachians	Downs 1944
	48.2/73.9	medium/good sites, mean 5 yrs, 15 trees, well-developed acorns	Gysel 1957
	19.0/23.5	medium/good sites, mean 5 yrs, 15 trees, sound acorns only	"
	(0)-213.9-(459.3)	ranges and mean 3 yrs study; oak-hickory forest, upland sites, E-C Illinois	Havera & Nixon 1980
	(0)-166.6-(300.8)	ranges and mean 3 yrs study; oak-hickory forest, ravine sites, E-C Illinois	"
	3.2/1620	mean, 15 samples, two consecutive yrs; upland streamside oak-hickory forest, Central Illinois	Johnson 1975
	36.5	kernel wt. only, one yr study, mixed second-growth hardwood and conifer; New York	Lewis 1982
Q. muehlenbergii	(1.8)-11.8-(17.9)	ranges and mean 3 yrs study; oak-hickory forest, ravine sites, E-C Illinois	Havera & Nixon 1980
Q. prinus	66.3/83.7	calculated from 7 yrs crops, from normal/exceptionally mature stands; Southern Appalachians	Downs 1944
	79.1	kernel wt. only, one yr study, mixed second-growth hardwood and conifer; New York	Lewis 1982
Q. stellata	5.6/10.1	large sample, two consecutive years, incs undeveloped/wormy acorns; oak-hickory forest, Missouri	Dalke 1953
3. Europe and the Mediterranean			
Q. cerris	(156.3)-296.9-(477.2) (dry wt)	range and mean, 4 yrs, includes cupules; N. Hungary	Tóth *et al.* 1985
Q. ilex	600-700	average yield over 3 million ha; oak-parkland (dehesa), S.W. Spain	Mazuelos Vela *et al.* 1961
	600-700	good area, (potential for 2500 kg/ha with good management), oak-parkland (dehesa), Sierra Morena, S.W. Spain	Parsons 1962

Table 14. Yield of acorns/unit area - individual species (concluded)

1.Western North America			
Area/Forest Type	Yield (kg/ha)	Comments	Source
S. California, montane woodland	1175	*Q. kelloggii* habitat; largest crop in memory	Bowyer & Bleich 1980
2. Eastern North America			
Missouri, oak-hickory forest	538.7	second-growth forest, 6 species included, good production year, incs undeveloped/wormy acorns	Dalke 1953
"	84.0	second-growth forest, 5 species included, poor production year, incs undeveloped/wormy acorns	"
Southern Appalachians	137.5-(c. 412.5)	mean and heavy crop yr, long-term, large-scale study, inc. wormy acorns, for an area of 850 ha	Downs 1944
"	164.1-(c. 492.3)	as the previous, for an area of 600 ha of normal/ exceptionally mature stands	"
Kentucky	0.4-55.1	min. and max. annual mean, 100 trees over 10 yrs, 7 spp. each of Lepidobalanus and Erythrobalanus	Feldhamer *et al.* 1989
S. Michigan	192.6/44.8	well-developed/sound only acorns, poor site, mean 5 yrs, *Q. velutina*	Gysel 1957
	272.2/137.7	well-developed/sound only acorns, medium site, 4 ha, mean 5 yrs, *Q. velutina* and *Q. alba*	"
	424.5/184.8	well-developed/sound only acorns, good site, 16 ha, mean 5 yrs, *Q. alba* and *Q. rubra*	"
E-C Illinois, oak-hickory forest	(126.6)-443.8-(735.4)	upland sites, 4 spp. present; ranges and mean, 3 yrs study	Havera & Nixon 1980
"	(148.9)-381.1-(676.4)	upland sites, 4 spp. present; ranges and mean, 3 yrs study	"
New York, mixed second-growth hardwood and conifer	139.4	kernel wt. only, one yr study, 3 spp. present	Lewis 1982
SE Missouri, bottomlands	(9.0)-171.5-(489.5)	range and mean, 12 yrs study, fully-developed sound acorns only, some of area artificially flooded, mainly *Q. palustris*, some *Q. phellos*	McQuilkin & Musbach 1977
"	(13.6)-176.5-(461.7)	ranges and mean, 5 yrs, *Q. palustris*	Merz & Brakhage 1964
SE Ohio, mixed hardwood forest	(0)-66.4-(169.3)	ranges and mean, 9 yrs, 505 ha site, mature forest, ravines and steep slopes, Lepidobalanus (*Q. alba* and *Q. prinus*)	Nixon *et al.* 1975
"	(5.7)-72.3-(195.7)	ranges and mean, 9 yrs, 505 ha site, mature forest, ravines and steep slopes, Erythrobalanus (*Q. coccinea*, *Q. rubra*, *Q. velutina*)	"
"	(20.4)-138.7-(196.9)	ranges and mean, 9 yrs, 505 ha site, mature forest, ravines and steep slopes, all species	"

Table 15. Yield of acorns/unit area - combined species (continued over)

Species	Yield (kg/ha)	Comments	Source
Arkansas Ozarks, upland hardwood	121.0 (dry wt)	mean of 8 yr study, from mixed-age stands	Segelquist & Green 1968
", upland pine-hardwood	77.3 (dry wt)	"	"
", cedar glade	19.0 (dry wt)	"	"
", stream-bottom hardwood	49.3 (dry wt)	"	"
", four forest types combined	(14.6)-109.8-(378.6) (dry wt)	ranges and mean 8 yr study, from mixed-age stands,, inc. *Q. velutina*, *Q. alba* with high yields, also *Q. rubra*, *Q. stellata*, and *Q. marilandica*	"
3. Europe and the Mediterranean			
S.W. Spain, oak-parkland (dehesa)	600-700	average yield over 3 million ha, *Q. ilex*	Mazuelos Vela *et al.* 1961
"	600-700	good area, Sierra Morena, SW Spain (potential for 2500 kg/ha with good management), *Q. ilex*	Parsons 1962
"	(66.4)-473.9-(1898.2)	ranges and mean of 8 different areas, one year, *Q. ilex*, *Q. faginea* and *Q. suber*	"
Monks Wood, Hunts., U.K.	≤645 (dry wt.)	years of heavy fall	Tanton 1965 (in Corbet 1974)

Table 15. Yield of acorns/unit area - combined species (concluded)

APPENDIX 4. COMPETITORS FOR THE ACORN CROP - FACTORS AFFECTING ACORN AVAILABILITY

4.1. INTRODUCTION

The genetic, environmental and physiological constraints on the potential size of the acorn crop, including those factors which cause loss of acorns from flowering to maturation, have been discussed in Appendix 3. However, some particularly significant causes of reduction in the potential crop size have not yet been considered fully - the damage or destruction of acorns by biotic agents. It is impossible to make a clear distinction between those factors which affect the matured crop and those which affect acorn production. For instance, insects may cause early abortion of acorns, as well as damaging the fully-ripened acorn. Many vertebrate predators may also remove or destroy acorns before they have ripened. However, the same species are often involved through the span of the acorn's life, and it is convenient to discuss all losses to predators together.

This section therefore comprises consideration of all reductions in the potential numbers of acorns which would otherwise be available as a human food source, either due to insect attack, disease, or removal by birds or mammals.

4.2. INVERTEBRATES

4.2.1. Introduction

Morris (1974) has noted that, in relation to both the acorn's importance to vertebrates, and the importance of the oak tree as a whole as an insect habitat, acorns are used by relatively few insect species, at least in Britain, and it seems likely that this is true also of oaks of other temperate areas, since the same small group of insects seems to be associated with oaks through at least this part of their range.

The most important invertebrate feeders on acorns fall into four groups, the Curculionidae (Coleoptera), Cynipidae (Hymenoptera), Lepidoptera, and Cecidomyiidae (Diptera) (Brown 1980; Darlington 1974; Jones 1959; Korstian 1927; Morris 1974; Winston 1956).

4.2.2. Coleoptera - Curculionidae

Probably the most common invertebrate feeders on acorns are the larvae of members of this group - the weevils. They are common predators on the seeds of most northern temperate

(and many other) members of both the Fagaceae and Juglandaceae, primarily as members of the genus *Curculio*, with some species of *Conotrachelus* (Boucher and Sork 1979; Korstian 1927).

Species of particular importance include *Curculio occidentalis*, recorded by Brown (1980) and Griffin (1980a) as one of the two most common acorn-boring insects in California; while in Britain *C. venosus* and *C. glandium* have been particularly noted (Jones 1959; Morris 1974). Korstian (1927) noted that 40 species of *Curculio* had been recorded, most of which fed on acorns.

Within the Curculionidae, only a part of the life cycle takes place within the acorn. The adult weevil drills a hole, usually just above the top of the cupule, before depositing her egg within the acorn, in late summer, and the weevil larva will feed from early autumn throughout the winter before leaving to pupate in the ground (Brown 1980).

4.2.3. Hymenoptera - Cynipidae

The gall-wasps, or Cynipidae, also particularly favour oaks as a habitat, and over 140 species have been recorded using various oak tissues just within the western United States (Brown 1980). Far smaller numbers appear to utilise acorns, and of 30-35 species found in Britain the only one which has been recorded doing so is *Andricus quercuscalicis* (cause of the knopper gall) (Darlington 1974). Other species which form galls on acorns within Europe include *Callirhytis* spp. on *Q. cerris* (Morris 1974), a genus which has also been recorded in the eastern United states (Korstian 1927). Despite the large numbers of species recorded on oaks most gall-wasps appear to be relatively harmless (Brown 1980).

The life cycle of cynipids on oak has been described by Darlington (1974).

4.2.4. Lepidoptera

Several groups of moth larvae may feed on acorns, and those recorded include members of the Tortricidae (Morris 1974), Eucosmidae (Jones 1959), and Olethreutidae, one member of which, *Melissopus latiferreanus*, may cause considerable damage in North America (Brown 1980; Griffin 1980a; Korstian 1927; Winston 1956). The adult *M. latiferreanus* lays eggs on the acorn surface and the larva bores in through the shell to feed. There may be two generations in one season, the first boring from July to September and the other from autumn through the winter (Brown 1980). Generally though, the effects of moth larvae on acorn crops are probably greater via their role as defoliators, which may be severe enough to reduce the tree's capacity for reproduction (Evans 1988).

4.2.5. Diptera - Cecidomyiidae

Some members of the Cecidomyiidae, or gall-midges, may also feed on acorns, or otherwise damage them, as secondary feeders (Morris 1974). Their presence may result in the formation of dwarfed acorns (Jones 1959).

4.2.6. Damage caused by invertebrates

The kinds of damage which are done to acorns by different larval feeders and other organisms have been described by Winston (1956), who examined all stages in the destruction of doomed acorns from their time on the tree until they became incorporated into soil humus. His study involved acorns of *Q. rubra* in Illinois, but since the types of organisms, and often the genera, involved seem to be so similar over the distribution of the oaks, his findings are probably generally applicable. Only the first two of Winston's five stages are relevant to acorns which might be potentially a human food source: stage one, the living nut on or off the tree, when any damage would not prevent development of the embryo, and stage two, the period of destruction of the embryo.

During stage one the most important source of damage was a species of weevil (*Curculio rectus*), which commonly consumed about half of the kernel before boring out to pupate. The moth larva *Melissopus latiferreanus* was second in importance, and could require as much as two or three acorns before completing development, so that any kernels infested had usually been totally destroyed by the time they dropped. In Winston's study a small percentage of acorns contained the larvae of a cynipid wasp (*Callirhytis* sp.), with two to eight larvae in each acorn, each in an individual gall in the embryo. During stage two the acorn kernel was destroyed completely or partially by those organisms already present, or by others. The exit holes of weevil larvae allowed scavengers in. The most important of these was another moth larva (*Valentinia glanduella*) which will eat the remainder of the kernel, and whose development takes about a year. Fungi are also often introduced at this stage, if not before, (see this Appendix, 4.3.) and mycetophages, including cheese mites and dipterous larvae, enter the acorn to feed on these. Much of this stage may take place while the acorn remains on the tree, but may continue for up to a year or more.

Korstian (1927) also examined in detail the kinds of damage produced by invertebrates on fallen acorns. In heavy infestations he noted that weevil damage was usually in excess of that by other insects. In about 75% of weevil-infested acorns over half of the cotyledons were destroyed to an extent which would curtail embryo development. Damaged acorns would subsequently decay more rapidly than others. Conversely, he noted that acorns infested with cynipids were usually capable of normal development, since their activity was

restricted by the gall formation, though this may not be the case with all species - the European knopper gall usually prevents subsequent germination of acorns.

The extent to which the acorn crop may be affected by insect damage has been estimated by many wildlife biologists and foresters, and most reports indicate the Curculionidae to be of overwhelming importance. Estimates of the proportion of the crop which may be destroyed by invertebrates may vary greatly between and within studies. Korstian (1927), for instance, noted the great variation in damage between different samples of the same species, and that damage could be very localised. Figures ranging from lows of around 0% (Griffin 1980a) or 10% damage (Christisen 1951) to highs of 80% (Brown 1980), or 'most' (Griffin 1971) have been recorded, and are summarised in Table 16.

4.2.7. Differential attack on oak species

Some of the physical or biochemical properties of acorns are thought to be in part defence mechanisms against insect or other predation (see Appendix 2). For example, the polyphenolic compounds present in acorns are commonly thought to be a deterrent, and the fact that concentrations of these vary from species to species implies that there might be a greater use of acorns with lower concentrations than of those with higher concentrations. The often thicker shells and higher tannin levels in the red-oak group have been suggested as reasons for lower predation by insects (e.g., Hilliard 1986; Koenig and Mumme 1987). An examination of the figures in Table 16 indicates that acorns of the red-oak group may possibly not suffer such extremes of high damage by insects (maximum 77% of the crop, cf. 98%). However, the range of overlap between the groups is great, and acorns of both groups in some cases suffer practically no damage. In addition, while Koenig and Mumme (1987) found a negative correlation between the percentage of acorns of different species damaged and their tannin content, data of Koenig (1980) showing the percentage of the acorn cotyledon eaten by insect larvae showed no such relationship. As with differential predation by vertebrates, discussed in this Appendix, 4.4.6.7., there is no clear consensus on this topic.

It has also been suggested that *Curculio* larvae and those of the Lepidopteran (Eucosmidae) *Ernarmonia* do not generally attack oak species whose fruits take two years to mature, and *Q. cerris* has been reported to suffer little in this respect (Jones 1959), but this does certainly not seem to be the case in the North American two-year species (the red oaks).

Physical barriers to predation also exist. Apart from shell thickness, which may explain why, for example, *Q. prinus* has sometimes been suggested to suffer little from insect attack (Miller and Lamb 1985), the cupule may deter insects as well as vertebrates. Kaul

(1986) described the development of the cupule, which encloses and protects the young acorn. Over time it becomes increasingly sclerified, and the development of tannins and crystals in both the cupule and the acorn shell are extra deterrents. In the tropical *Cyclobalanopsis* sub-genus Kaul noted that the cupule seemed to provide adequate protection during the younger stages of development, but that weevils appeared in mature acorns. Adult weevils make the holes in which their eggs are laid just above the top of the cupule (Jones 1959), and it may be here, where the acorn has most recently emerged from its protective surrounding, that the acorn shell is at its most vulnerable.

4.2.8. Variability between years in insect use of acorns

There have been suggestions in the literature that the numbers of acorns damaged by both invertebrate and vertebrate predators varies between years, and particularly that damage is greater in years with small crops (Burns *et al.* 1954; Christisen 1955; Downs 1944).

McQuilkin and Musbach (1977) found that, though there was a considerable range in the numbers of insect-infested acorns between years, this range was much less than that of the total crop, or the number of fully matured, undamaged acorns - effectively the damage remained about the same every year, regardless of the size of the crop. As a percentage of mature acorns, therefore, the quantity of wormy acorns increased as crop size decreased. Those studies which have explicitly examined this variable have produced mixed results, however. Gibson found greater proportional losses to insects in years of low production in one study but not in another (Gibson 1971, 1972, cited in Sork and Boucher 1977).

4.2.9. Factors affecting insect damage

Apart from any differences in damage to acorns of individual species, or between years, other factors may introduce variability into the extent of insect predation.

Factors relating to the ecology of the insect species concerned could be of importance. For example, although the presence of the knopper gall, which appeared in Britain in the 1960's, has sometimes caused serious depletion of the acorn crop in recent years it does not apparently do great damage on the continent where it has a longer history, and the gall-wasp responsible has its own predators and parasites (Darlington 1974).

Local environmental variations could have some influence on the extent of damage. McQuilkin and Musbach (1977) found higher insect damage to *Q. palustris* on unflooded areas than on areas flooded artificially during the oak's dormant season, and suggested the likely reason was the fact that *Curculio* spp. (the principal offenders) overwinter in the soil

and would be killed by flooding. However, since the total yield was lower on flooded areas the absolute numbers of available non-insect-eaten acorns was about even.

4.3. PATHOGENIC ORGANISMS

Acorns, especially those already damaged by insects, or perhaps other factors such as frost or desiccation (Murray 1974), may be susceptible to infection by pathogenic organisms, which could further devalue their use as a human food source. Winston (1956) noted the introduction of parasitic fungi (including *Penicillium* and *Fusarium*) by insect feeders, though they were also able to enter unaided via the micropyle, or around the attachment scar. He also noted differential attack on oak species, probably related to local environmental factors. Acorns of *Q. rubra* in the floodplain forest were more subject to decay by fungi than those of *Q. velutina* and *Q. alba* in drier upland stands.

Bacterial pathogens may also infect acorns, especially those already damaged by insect borers, and 'drippy nut', a sour fermented liquid produced by *Erwinia quercina*, which drips from the acorn has been recorded in California, especially on acorns of *Q. agrifolia* and *Q. wislizenii* (Brown 1980; Raabe 1980).

Although most pathogens attack already devalued acorns, they may also affect acorns in which insect larvae have failed to develop. Korstian (1927) noted that many mature acorns with ovipositor scars were mouldy, especially with *Penicillium* spp. He also noted parasitic fungi (*Botrytis* and *Fusarium*) attacking acorns in the early stages of germination.

Murray (1974) lists several fungal pathogens which have been found attacking acorns in Europe and America, and notes that a particular feature is their non-specificity, either to particular oak species or to the genus itself. Most will attack the fruits of other trees, especially *Castanea* and *Fagus*, and most are also very widespread.

4.4. VERTEBRATES

A large number of studies have demonstrated that acorns are one of the most important foods for wildlife, both in terms of the quantities utilised and the numbers of species feeding on them. Their value perhaps relates particularly to the timing of their availability and their abundance; but many studies have also demonstrated that they are important not just as a seasonal resource, but may be used more-or-less year round by some species.

As with other biological data, although much of the evidence comes from the United States and Europe, many of the important families and genera are similarly distributed through

woodlands and forests of other parts of the world, and analogous relationships probably occur in these less well documented regions.

4.4.1. Numbers of species eating acorns

Lists of vertebrate use of acorns for some areas have been compiled by several authors, though many comment that their results are by no means comprehensive, and this is especially so with regard to the species of oaks that are utilized. A survey of wildlife use of oaks undertaken in the late 1930's in North America found that their importance surpassed that of practically all other woody plants - 186 birds and mammals ate some part of the oak, and acorns were eaten by a considerable number (unfortunately not specified), and were often classed as favourite foods (Van Dersal 1940). In California at least 22% (37) of terrestrial mammals eat acorns (Barrett 1980). Of 110 bird species using Californian oak habitats during the breeding season at least 30 (27%) eat acorns (Verner 1980). Miller and Lamb (1985) state that in the eastern United States at least 49 species of bird and mammal utilize acorns. Corbet (1974) records 15 mammals found in Britain (i.e., about 50% of terrestrial mammals) which make extensive use of acorns, and notes that this is true of all those British woodland mammals which are not wholly insectivorous or carnivorous. He also records acorn use by four eastern Asian species introduced to Europe.

4.4.2. Coincidence of range of oaks and acorn-eaters

Van Dersal (1940), commented that for some vertebrates the importance of acorns in the diet was such that their ranges appear to coincide with that of oaks. This probably applies to many of the species discussed below as important acorn eaters, the most notable being the acorn woodpecker (see this Appendix, 4.4.5.2.1.).

4.4.3. Relationships between fluctuations in acorn crop size and vertebrate population densities

In general those animals which depend to some extent on the fruits or seeds of masting species tend to have greater fluctuations in their numbers than species which utilize more regular food sources, particularly since such crops usually appear (or do not appear) at a time when other food sources are poor. Such fluctuations may be due to population failure or diminishment, or migration to other areas. Though few vertebrate species are totally dependent on acorns, and most which favour acorns can utilize other food sources if they are not available, several could probably not maintain normal population densities without a fairly regular supply. Among others, numbers of bear, deer (at least in North America), some squirrels, European mice and bank voles, and the North American red-headed

woodpecker may fluctuate in density according to the annual crop of mast (Barrett 1980; Burns *et al.* 1954; Goodrum *et al.* 1971; Jensen 1982; Kenward and Holm 1989; Nixon and McClain 1969; Short 1976; Smith and Scarlett 1987; Trail 1980; Van Dersal 1940).

Animal-acorn relations may of course be important on levels other than that of the individual species. The importance of oaks in general to wildlife makes this difficult to estimate, though one study of the relations of wildlife numbers to various habitat types of the California black oak (*Q. kelloggii*) concluded that the most important factor governing total wildlife abundance and use of the different habitats was the availability of acorns (Kerns 1980).

4.4.4. Frequency and abundance of acorns in the diet

Further indication of the importance of acorns to some vertebrates comes from studies which have attempted to estimate the quantities of acorns consumed as a proportion of total diet, often from examinations of stomach contents of dead animals. Many of the earlier studies focussed on game animals, but those by foresters, wildlife biologists, or ecologists have examined those species to whom acorns are apparently most important, and, for example, whose acorn predation might therefore affect oak regeneration. Though the precise results of many of these studies, especially the earlier ones, may be questionable on methodological grounds (since the identification of food remains, and estimation of diet from stomach contents is subject to many vagaries - see, e.g., Baumgartner and Martin 1939; Koenig 1980; Korschgen 1981), much of the evidence is supported on a general basis by anecdotal and non-quantitative evidence and field observations, and at least gives a fairly representative idea of the most important acorn-eaters. Some of the estimates that have been made are given in the following section, as they may provide an indication of the likely extent of competitive interaction species might be expected to have with people exploiting acorns.

4.4.5. Species of importance

4.4.5.1. Mammals

Scientific and common names of mammals follow Corbet and Hill (1986).

4.4.5.1.1. Sciuridae

Numerous observations have been made in eastern North America of the importance of acorns in the diet of eastern grey squirrel (*S. carolinensis*) and eastern Fox squirrel (*S.*

niger), including those by Cypert and Webster (1948), Davison (1964), Downs (1944), Havera and Smith (1979), Korstian (1927), Lewis (1982), Short (1976), Smith and Follmer (1972), Van Dersal (1940), Wolgast and Stout (1977a), and Wood (1938).

Some of the most commonly cited quantitative estimates of importance to these species are those of Goodrum *et al.* (1971) and Goodrum (1972, cited in Keller 1987) who suggested that acorns are likely to form between a half and three-quarters of the diet, and that acorns were fed on every month of the year. Another study found acorns to be third in importance in the diet, following hickory and beechnuts (estimated from both occurrence and total volume consumed in stomach contents). Unlike the other nuts, however, acorns were used more extensively throughout the year, and were also used in greater quantities than any other foods through the winter months (Nixon *et al.* 1968).

One study which cast doubt on the importance of acorns, and other mast crops, in squirrel diet is that of Havera and Nixon (1980) in Illinois, who examined the relationship between acorn crop size and squirrel body weights over the winter, and concluded that they usually managed to maintain adequate nutrition, even when crops were quite small. They suggested that the role of mast crops in over-wintering was perhaps not as critical as has previously been suggested, as there generally seem to be sufficient alternative foods around, but their study took place over only three years, and they did suggest that in a severe winter, if mast crops had failed to a greater extent than they did, the effects might have been noticeable.

In western North America other squirrels take the place of principal mammalian arboreal feeders. One study of the western grey squirrel (*Sciurus griseus*) undertaken in the wild in California, cited by Potter and Johnson (1980) found that, of a daily intake of around 100g of food, acorns constituted 9.6% in July and 71.3% in December, averaging 50.9% over 11 months (made possible by storage behaviour). Passof *et al.* (1985) also suggested that acorns probably make up about half the diet of this squirrel for six months during abundant acorn years.

Other members of the Sciuridae recorded using acorns in North America include chipmunks (*Tamias* spp.) which will feed on acorns where available (Barrett 1980; Korstian 1927; Passof *et al.* 1985; Van Dersal 1940); flying squirrels (*Glaucomys* spp.) (Barrett 1980; Cypert and Webster 1948; Van Dersal 1940); ground squirrels (*Spermophilus* spp.), (Barrett 1980), including the rock squirrel (*S. variegatus*) (Ridley 1930), and the California ground squirrel (*S. beecheyi*), which together with the western grey squirrel will bury individual acorns, and may also store large numbers in underground chambers (Duncan and Clawson 1980; Griffin 1971).

Squirrels appear to be particularly closely associated with oaks even in the tropics, where they do not apparently store acorns. Ridley (1930) noted that in the Malay peninsula wherever species of *Quercus* and *Lithocarpus* occurred squirrels were always present, and that in the hill forests with few or no squirrels there were fewer oaks. Western European forests, on the other hand, are particularly deficient in squirrels in relation to their importance in other oak-inhabited areas, and the only indigenous species, the Eurasian red squirrel (*Sciurus vulgaris*), at the present day at least, appears to prefer conifers, beech or hazel, though it certainly includes acorns in its diet, and will store acorns by burying them (Corbet 1974; Kenward and Holm 1989; Ridley 1930; Watt 1919). Feeding tests have shown that this species is less able to digest acorns than is the introduced eastern grey squirrel (Kenward and Holm 1989).

4.4.5.1.2. Other Rodents

Other members of the Order Rodentia, may feed on acorns extensively, though probably not in such large quantities.

Some of those recorded as acorn eaters are as follows:

Geomyidae - Botta's pocket gopher (*Thomomys bottae*), in western North America (Barrett 1980; Griffin 1980a).

Muridae - North American deer mice (*Peromyscus* spp.) (Barrett 1980; Cypert and Webster 1948; Korstian 1927) which sometimes also store acorns (Griffin 1971); the dusky-footed woodrat (*Neotoma fuscipes*) (Barrett 1980; Passof *et al.* 1985); the European bank vole (*Clethrionomys glareolus*) (Corbet 1974; Evans 1988; Jones 1959; Watt 1919); European wood mouse (*Apodemus sylvaticus*) and yellow-necked mouse (*A. flavicollis*) (Corbet 1974; Evans 1988; Jones 1959; Watt 1919); European rats (*Rattus* spp.) (Ridley 1930); fat dormouse (*Glis glis*); and hazel dormouse (*Muscardinus avellanarius*) (Corbet 1974; Watt 1919).

4.4.5.1.3. Lagomorphs

Members of the Order Lagomorpha are generally more closely associated with open country than are the squirrels and many other rodents, but they may nevertheless sometimes feed on acorns quite heavily. Species recorded doing so include (all in the family Leporidae) in North America several rabbits (*Sylvilagus* spp.) (Barrett 1980; Goodrum *et al.* 1971; Korstian 1927) and the black-tailed jack rabbit (*Lepus californicus*)

(Barrett 1980); and in Europe the European rabbit (*Oryctolagus cuniculus*) (Corbet 1974; Watt 1919), and the brown hare (*Lepus europaeus*) (Corbet 1974).

4.4.5.1.4. Deer

A particularly widespread and important group of acorn eaters are the deer (Artiodactyla: Family Cervidae). Several studies have examined the quantities of acorns present in deer diets, and in some species very heavy seasonal use of acorns is recorded.

4.4.5.1.4.1. Western North America

In one study of the mule or black-tailed deer (*Odocoileus hemionus*) of western North America Menke and Fry (1980) found acorns appearing as more than 5% of rumen contents from July, increasing rapidly through September (38.3%) and October (33.3%), followed by a sharp drop in November to 6.9%. Only traces of acorns remained in rumen samples until March, and then were absent entirely through the spring. In September acorns constituted 85-100% of the total volume of food in some samples, though the frequency of occurrence was highest in October, with quantities ranging from 10-20% of volume. Another study in southern California found that deer ate on average 315 acorns a day during the autumn (equivalent to 1.21kg dry weight/deer/day), and acorns made up a large percentage of the contents of all rumens examined (Bowyer and Bleich 1980). Potter and Johnson (1980) found that of c. 2.3kg food eaten per day, in a good mast year about half of this from October to December was acorns, with values ranging from 11-76%. Passof *et al.* (1985) noted that acorns make up 15-20% of diet of some deer during the 6 month summer-autumn period, and may constitute 50% of winter food for migratory deer; and Scrivner *et al.* (1988) have also noted that acorns are important in the diet for about three months of the year.

4.4.5.1.4.2. Eastern North America

In the eastern United States acorns have similarly been observed to be of importance in the diet of the White-tailed deer (*O. virginianus*). One study by Goodrum *et al.* (1971) in December showed acorns ranging from 16-98% of rumen contents, and another study undertaken in November showed acorns to comprise 50-100% of rumen contents. They also cite Short *et al.*'s (1969) findings of 93% of rumen contents in November for this species in Texas. Acorns may also be eaten for much of the year. Lay (1965, cited in Goodrum *et al.* 1971) found acorns in deer pellets for 10 months of the year, though they were especially common from September to February; Christisen and Korschgen (1955, cited in Goodrum *et al.* 1971) found substantial amounts in rumens from September to

May; and Pearson (1943) found acorns to constitute nearly half of all rumen contents over 6 years in Alabama. Another long-term study of deer in Missouri determined that acorns from 11 species of oaks made up 38.6% of the total food consumed over twelve years. The heaviest use occurred in the year of heaviest production, when acorns occurred in 93.8% of stomachs, as 80.1% of the total volume of food. In the following year of very low crops they constituted only 8.5% of food consumed. In a year of average production they occurred in intermediate quantities. Quantities varied over the area studied, and acorns were most important in the Ozarks where they commonly comprised half to three fourths the annual diet (averaging 53.5%), less important in the river valleys (30.7%) and least used by deer of the prairie (25.3%). Acorns became available in September and were used heavily then, continuing until May when use became minimal until September (Korschgen 1962).

Others who have commented on the extensive use of acorns by the North American deer include Downs (1944), Duvendeck (1962), Korstian (1927), Pekins and Mautz (1988), Van Dersal (1940), Wolgast and Stout (1977a). One other North American Cervid, the Moose (*Alces alces*), may also eat acorns (Barrett 1980).

4.4.5.1.4.3. Europe

In Europe, the Red deer (*Cervus elaphus*), Roe deer (*Capreolus capreolus*), and especially the Fallow deer (*Cervus dama*), eat acorns (Corbet 1974; Jones 1959; Ridley 1930; Watt 1919); and three eastern Asian species, the Sika (Cervus nippon), Chinese muntjac (*Muntiacus reevesi*) and Chinese water deer (*Hydropotes inermis*), have been noted eating acorns since their introduction to Europe (Corbet 1974).

4.4.5.1.5. Other Artiodactylids

Other important Artiodactylid acorn eaters include some of the pigs (Suidae) and peccaries (Tayassuidae). The European wild boar (*Sus scrofa*) is a very heavy seasonal user of acorns, through at least the temperate broad-leaved woodland part of its range, extending from western Europe to south-eastern Siberia, and up to 5kg of acorns have been found in one stomach (Corbet 1974; Jones 1959; Ridley 1930; Thiel 1957; Watt 1919). This species also feeds heavily on acorns where it is introduced, such as North America, either as the wild type, or as feral members of the domesticated pig (*S. domesticus*) (Barrett 1980; Henry and Conley 1972; Korstian 1927; Passof *et al.* 1985). The collared peccary (*Tayassu tajacu*) of Southern Arizona feeds on acorns of several oaks (Eddy 1961).

The other Artiodactylid family which contains acorn-eating species is the Bovidae. The (now very restricted in distribution) European bison (*Bison bonasus*), and the extinct ancestor of domestic cattle, the aurochs (*Bos primigenius*) are, or were, both thought to be primarily species of deciduous forest (Corbet 1974) and almost certainly ate acorns. Domestic cattle (*Bos taurus*) will certainly eat acorns when permitted to roam in areas where they are available, both in Europe and in North America (Duncan and Clawson 1980; Korstian 1927; Watt 1919). Wild goats (*Capra aegagrus*) and sheep (*Ovis orientalis*) are thought to be principally creatures of mountainous country and steppe respectively (Garrard 1984), and the extent to which acorns may have occurred in their diet is uncertain, though the fact that the domestic goat (*C. hircus*), if not the domestic sheep (*O. aries*), feeds, and is fed on, acorns in parts of Southwest Asia, suggests that they might have comprised part of the diet of the wild species.

4.4.5.1.6. Carnivora

Acorns may be very important in the diets of some of the more omnivorous of the Order Carnivora. Of the bears (Ursidae) the American black bear (*Ursus americanus*) (Barrett 1980; Korstian 1927; Landers *et al.* 1979; Van Dersal 1940; Wolgast and Stout 1977a), and the brown bear (*Ursus arctos*) (Corbet 1974), are extensive users of acorns.

Other Carnivora recorded eating acorns include, in the Canidae, the North American grey fox (*Vulpes cinereoargenteus*) (Goodrum *et al.* 1971), and the raccoon-dog (*Nyctereutes procyonoides*) of Eastern Asia (Corbet 1974); in the Procyonidae, the ring-tailed cat (*Bassariscus astutus*) in California (Barrett 1980), and the common raccoon (*Procyon lotor*) throughout North America (Barrett 1980; Goodrum *et al.* 1971; Van Dersal 1940); and, in the Mustelidae, the Eurasian badger (*Meles meles*) (Corbet 1974), and the North American striped skunk (*Mephitis mephitis*) and spotted skunk (*Spilogale putorius*) (Barrett 1980).

4.4.5.2. Birds

Scientific and common names of birds follow Howard and Moore (1991).

4.4.5.2.1. Woodpeckers [Picidae - Piciformes]

Among the birds occurs one species whose lifestyle is perhaps more closely related to acorn use than that of any other vertebrate. This is the acorn woodpecker (*Melanerpes formicivorus*), distributed through the oak woodlands of the Pacific coast of North America

and with a range extending to the southernmost extreme of oak distribution in the Colombian Andes (Kattan 1988).

The quantities of acorns eaten by this species have been estimated in various studies, beginning with that of Beal (1910, cited in Van Dersal 1940), who estimated an intake of 52.4% of the diet over a year, except for February, April and May, with a high of 93.6% in November. Verner (1980) similarly suggests a figure of more than 50% of the diet over a year; though more detailed recent studies (Koenig 1980) suggest such high figures may be over-estimates, and that acorns probably make up about 50% of the diet over winter, and about 25% over a year. Nevertheless, all studies agree that acorns are essential, especially to overwintering survival, and studies have been made of correlations with reproductive success, range of distribution and with social behaviour in relation to various measures of acorn availability over the range of the species (see also Bock and Bock 1974; Koenig and Mumme 1987; Koenig and Heck 1988; Trail 1980).

Other Californian woodpeckers that feed on acorns include Lewis' woodpecker (*Melanerpes lewis*), an arboreal feeder, which has nomadic rather than territorial behaviour and does not store acorns, but may form large feeding flocks in the autumn, and in whose diet acorns have been estimated to comprise 10-25% of the total (Koenig 1980; Verner 1980); plus several species of *Picoides* (Verner 1980).

In 1940 Van Dersal noted 14 species of woodpecker which had been recorded as acorn eaters within North America. In the east the red-headed woodpecker (*Melanerpes erythrocephalus*) and the red-bellied woodpecker (*Melanerpes carolinus*) have been recorded removing large quantities of acorns from trees (Cypert and Webster 1948; Smith and Scarlett 1987). Others who have commented on extensive acorn predation from trees by various woodpeckers include Goodrum *et al.* (1971), McQuilkin and Musbach (1977), and Wolgast and Stout (1977a).

Another member of the Picidae, the common flicker (*Colaptes auratus*) found throughout North America feeds on acorns in the trees (Cypert and Webster 1948; Verner 1980).

4.4.5.2.2. Jays and other Corvidae [Passeriformes]

Several Corvidae may be important acorn eaters. Blue jays of eastern North America (*Cyanocitta cristata*) will store acorns and have been noted feeding extensively on them by Cypert and Webster (1948), Goodrum *et al.* (1971), Korstian (1927), McQuilkin and Musbach (1977), Smith and Scarlett (1987), Van Dersal (1940), who recorded ten species, and Wolgast and Stout (1977a).

In California and the west the scrub jay (*Aphelocoma coerulescens*) is an important acorn eater. Scrub jays may form feeding assemblages in the autumn to harvest from areas with heavy crops, and will store acorns in the ground (Griffin 1971, 1980a; Koenig 1980). Van Dersal (1940) quotes (from Beal 1910) a figure of 38.2% of the year's diet consisting of acorns; while Verner (1980) suggests that acorns comprise from 25-50% of the diet of this species. He quotes a similar figure for Steller's jay (*Cyanocitta stelleri*), for which Van Dersal (1940 again citing (Beal 1910) quotes 42.5% over the year, with acorns forming 99% of the diet in January.

The yellow-billed magpie (*Pica nuttalli*), is another Californian species which includes an unknown portion of acorns in the diet, and also stores acorns in the ground (Griffin 1971; Verner 1980). Other Corvidae, especially the American crow (*Corvus brachyrhynchos*), which harvests acorns from the trees in flocks during the autumn, but does not apparently store acorns, is also found (Griffin 1980a; Koenig 1980; Verner 1980); and this species also commonly eats acorns in the eastern United States (Goodrum *et al.* 1971; Korstian 1927). The North American subspecies of the common raven (*C. corax*) also feeds on acorns (Verner 1980).

In Europe the jay (*Garrulus glandarius*) is an important seasonal feeder on, and disperser of, acorns, and removes them from the trees in large quantities, to subsequently store them in the ground, as do carrion crows (*Corvus corone*), rooks (*C. frugilegus*), and common ravens (*C. corax*) (Evans 1988; Jones 1959; Ridley 1930; Watt 1919). As Flegg and Bennett (1974) comment, relatively few British (or European) birds are designed to cope with acorns, and the species mentioned do not specialise in their feeding on acorns, but capitalise on them when available.

4.4.5.2.3. Other arboreal feeders

4.4.5.2.3.1. Columbiformes [Columbidae]

The wood pigeon (*Columba palumbus*) is another European species which will utilise acorns in vast quantities, preferring them to all else when they are plentiful (Evans 1988; Jones 1959; Ridley 1930; Watt 1919). They do not store acorns, except temporarily in their crops, which may hold from 60-70 acorns weighing 200g (Jones 1959). In California, the band-tailed pigeon (*C. fasciata*) behaves similarly, and forms flocks at acorn harvest time, with acorns constituting 25-50% of the diet (Koenig 1980; Passof *et al.* 1985; Verner 1980). Mourning doves (*Zenaida macroura*) will also feed on acorns in small quantities but they do not seem to be a preferred food (Davison and Sullivan 1963).

4.4.5.2.3.2. Passeriformes

Several Passeriforme birds also feed on acorns in the trees, including the grackles of eastern North America (*Quiscalus* spp. - Icteridae) (Cypert and Webster 1948; Van Dersal 1940); and nuthatches (*Sitta* spp. - Sittidae) (Van Dersal 1940), especially the white-breasted nuthatch (*Sitta carolinensis*) for which acorns may constitute 10-25% of the year's diet (Passof *et al.* 1985; Verner 1980).

Other Passeriformes recorded feeding in small quantities on acorns, which might use fallen acorns or those on the trees, include, in Europe, the chaffinch (*Fringilla coelebs*) (Fringillidae) (Evans 1988); blackbird (*Turdus merula*) (Turdidae) (Ridley 1930); the New World blackbirds (Icteridae) (Korstian 1927); and members of the Paridae - the North American titmouse and chickadee (*Parus* spp.) (Van Dersal 1940); and Troglodytidae - the Carolina wren (*Thyrothorus ludovicianus*) (Cypert and Webster 1948).

4.4.5.2.4. Ground-feeding birds

There are several groups of birds for whom fallen acorns are important food, principally members of the Galliformes and the Anseriformes.

4.4.5.2.4.1. Galliformes

Acorns in the diet of the north American common turkey (*Meleagris gallopavo*) (Phasianidae) (Van Dersal 1940), may comprise 25-50% for at least 6 months of the year, and feeding continues for most of the year if acorns are available (Goodrum *et al.* 1971; Korstian 1927; Passof *et al.* 1985; Verner 1980; Wolgast and Stout 1977a).

In North America quail (sub-family Odontophorinae) of several kinds (Van Dersal 1940) also eat acorns, principally in autumn and winter, though again they will be included in the diet more or less year-round if available. In the east, observations by Goodrum *et al.* (1971) included that of the northern bobwhite (*Colinus virginianus*) the contents of whose crops, measured over 9 years from November to February, varied by year from 5% to 37% of volume in crops (averaging 15% over the whole study), with variation in frequency of occurrence of acorns from 12% to 46%. They cite another study which found acorns present in bobwhite crops every month of the year except May and September, comprising up to 16% of the diet in April, though they were principally a seasonal food source. Van Dersal (1940) cites several studies of bobwhites showing quantities ranging from 16 or 17% in March/April, with from 2.9 to 6% acorns in the diet in the autumn and winter

months. Wolgast and Stout (1977a) also note the importance of acorns in the diet of this species.

In California Potter and Johnson (1980) estimated that of a total of 9g of food per day eaten by California and mountain quail (*Lophortyx californica* and *Oreortyx picta*) acorns probably constituted half the intake over the three months of peak availability; while Verner (1980) estimates acorn intake at about 10-25% of the total diet.

Other significant Galliforme acorn eaters include, in Europe, common pheasants (*Phasianus colchicus*) (Watt 1919); and in North America, several species of grouse (sub-family Tetraoninae) (Van Dersal 1940; Wolgast and Stout 1977a). Servello and Kirkpatrick (1989) cited studies of ruffed grouse (*Bonasa umbellus*) in the southeastern United States where acorns constituted 63-65% of the diet, with individuals consuming even greater amounts when acorns were particularly abundant. Probably this figure is for the peak period of abundance, since studies cited by Van Dersal (1940) suggest around 5-10% of the diet in autumn and winter, and a similar figure for year-long consumption. Korschgen (1966) also noted heavy feeding by ruffed grouse in a good mast year, with most acorns eaten in December, but comprising more than half the diet in October, November, March and April, with acorns used in some amounts throughout the year. In a year of near failure of acorn crops there was only 11% utilization in October and November, and traces over the winter.

4.4.5.2.4.2. Anseriformes

Acorns of some oaks, principally river valley or bottomland species may be quite important seasonally, or occasionally, in the diets of waterfowl (Van Dersal 1940), including Canada (*Branta canadensis*) and other geese (*Branta* and *Anser* spp.) (Passof *et al.* 1985; Van Dersal 1940), mallard (*Anas platyrhynchos*), North American black duck (*A. rubripes*), northern pintail (*A. acuta*), ring-necked duck (*Aythya collaris*), (Delnicki and Reinecke 1986; McQuilkin and Musbach 1977; Passof *et al.* 1985; Ridley 1930), and especially wood duck (*Aix sponsa*) where acorns may comprise 25-50% of the diet (Verner 1980), though feeding may be much reduced in years of regional mast failure (Landers *et al.* 1977).

4.4.6. Characteristics of vertebrate use of acorns

Some features of vertebrate use of acorns may be of special importance in relation to their role as competitors with humans for the acorn crop. These are discussed below.

4.4.6.1. Arboreal and ground feeders

Vertebrates which eat acorns can be divided, more or less, into two categories in relation to their potential effect as competitors with humans for acorn utilisation. Many animals are able only to feed on acorns once they have fallen to the ground, whereas some are capable of arboreal feeding (though many of these will also feed on fallen acorns). The effects of arboreal feeders are likely to be of more importance to humans hoping to harvest acorns, than are those which only feed on the ground, simply because they may remove much of the potential harvest before people get to it, and sometimes well before the acorns are fully ripe. Tanton (1965 cited in Corbet 1974) for instance, noted that use of acorns on the ground by rodents could vary considerably according to the extent to which the crop had been consumed by others before it fell, and recorded extremes of 92% and 8% of the crop removed from trees by wood pigeons. Nevertheless, feeding on acorns on the ground may also be significant, as a much larger group of animals is involved, and maximum feeding obviously coincides very closely with the period at which acorns are falling and are therefore theoretically easiest to obtain. Any people collecting acorns from the ground at this time, or later in the season, would be in direct competition with ground-feeding animals.

Most birds are evidently capable of arboreal feeding, and those which are primarily ground-feeders have been indicated in this Appendix, 4.4.5.2.4. Of the mammals squirrels are probably the most important arboreal feeders, and this may include the so-called ground squirrels (Duncan and Clawson 1980). Squirrels will harvest green acorns as early as August (Nixon *et al.* 1968; Wood 1938). Some of the other rodents listed, e.g., *Apodemus* spp., especially *A. flavicollis* (Corbet 1974) will also feed in the trees. In Europe the fat dormouse is an arboreal feeder to a greater extent than the common hazel dormouse, which tends to favour the shrub-layer, so acorns are likely to be more important in its diet (Corbet 1974). Some arboreal feeding may be undertaken by deer on small and shrub oaks, or on the lower branches of tree oaks. Goodrum *et al.* (1971) observed white-tailed deer in Louisiana eating acorns of *Q. marilandica* directly from the trees.

Some workers have attempted to estimate the differing losses of acorns to arboreal and non-arboreal feeders These are indicated on Table 16, and discussed further in 7.3.

4.4.6.2. Acorn storers

Another important categorisation of acorn eaters in relation to potential human use concerns those species which store acorns for future use. Though this behaviour might occasionally be of advantage, since stores, especially of those species which accumulate large supplies

of acorns in one place, might be a useful source of supplies for human raiders (see 3.2.1.3.1.), in general animals which store acorns will be strong competitors for acorns, since they will remove proportionately more of a crop during the period of peak availability than they might otherwise apparently require. This situation is exacerbated by the fact that most of those species which store acorns in large numbers are also arboreal feeders (e.g., the squirrels and other rodents, woodpeckers and jays).

Many rodents, and especially squirrels, will bury individual acorns, and may also occasionally store large numbers in underground chambers. One squirrel storage chamber in California was found to contain 203 acorns (Griffin 1971). Of European species other than squirrels, the woodmice (*Apodemus* spp.) and Bank vole cache acorns under logs and in burrows (Corbet 1974).

Acorn storers among the birds include some of the jays, (e.g., blue jay and scrub jay, as well as the European jay) which tend to bury individual acorns, and woodpeckers, including the red-headed woodpecker, and the acorn woodpecker, whose storage behaviour may be limited by the availability of suitable storage trees, and the holes made in them, each of which takes an individual acorn (Koenig and Heck 1988).

Not all storers can be assumed to be equally important, or equally dependent on acorns. For example, in Missouri, Smith and Scarlett (1987) found that, unlike that of the red-headed woodpecker, populations of blue jays did not fluctuate significantly in relation to the size of acorn crops. This species therefore seems to be less dependent on acorns than the woodpecker, and more readily uses alternative foods.

4.4.6.3. Physiological storers

An alternative strategy adopted by some animals relating to the massive abundance of acorns and other mast crops in the autumn is to 'store' acorns by consuming large quantities and producing layers of fat for over-wintering. To a certain extent this probably applies to all species which use acorns, but it is especially important for those species that undergo hibernation to any degree, and these in particular may utilize a disproportionately large quantity of acorns at the time of peak abundance. Examples are, in Europe, the bear and badger, which both make extensive use of acorns in autumn, and dormice. The North American racoon and the East Asian racoon dog also hibernate lightly, and fatten up on acorns. In most non-hibernating species there is probably a more even use of acorns through the winter (Corbet 1974).

One species which does not hibernate, but which has great autumn fattening ability is the wild boar. The suggestion has been made that this species is able to fatten to such a great extent because it does not require great mobility to avoid predators unlike, for example, squirrels, which use the alternative strategy of external storage (Corbet 1974).

The fallow deer is another especially avid acorn eater, possibly because the period of peak acorn availability follows closely on the rutting season during which the males eat very little, so that their subsequent quick recovery in preparation for winter is probably to a considerable extent dependent on the acorn crop (Corbet 1974).

4.4.6.4. Effects of other mast species on acorn utilization

The extent to which the acorn crop is used by some animals may depend to some extent on the availability of alternative foods, especially the 'nuts' of other masting species - principally other members of the Fagaceae (such as *Lithocarpus*, *Castanopsis*, *Castanea*, and *Fagus*), and the Juglandaceae (*Carya* and *Juglans*).

For example, the grey squirrel introduced to Britain is said to prefer *Castanea* and *Fagus*, and to exhaust these first before turning to acorns. The Eurasian red squirrel is also said to prefer beech (as well as hazel), as are voles and mice, though often the correlation seems to be with the local availability or relative sizes of the crop (Corbet 1974; Jones 1959).

Nixon *et al.* (1968), also examined preferences of grey and fox squirrels for different nuts, and found an apparent preference for hickories, then beech, with acorns third (followed by black walnut and yellow buckeye), apparently correlated very closely with the order of ripening. Acorns, however, were the most heavily-used species through the winter, and some green acorns were observed being harvested even before green hickories. Smith and Follmer (1972) observed a very similar pattern of use, with hickories eaten in autumn and spring. They suggested that, while hickories are a high energy food and take up little room in the stomach, enabling high mobility, they take longer to crack than acorns. Acorns would therefore be preferred over winter, when it is advantageous to remain out of the nest for as little time as possible, and when large quantities of the lower energy acorns in the stomach would not be a disadvantage once back in the nest.

Davison (1964) also examined the preferences of eastern grey squirrels, and cites another study indicating that availability was the most important factor under natural conditions. His own studies involved observing which of foods presented to squirrels in the wild were preferentially eaten, and he found that acorns (of 24 species) were apparently as favourable as most of the hickories, beech, hazelnuts, and walnuts (and possibly more so); with two

hickories (*Carya cordiformis* and *C. aquatica*) less favoured, and *Aesculus* spp., left more-or-less uneaten.

Korschgen (1981) found that though acorns of 11 species were consumed relative to their availability, consumption of nuts of seven species of Juglandaceae, by fox and grey squirrels, greatly exceeded the amounts expected from forest composition. A similar result was obtained by Lewis (1982) in a study of grey squirrels, where nuts of *Carya glabra* were eaten, overwinter, as a greater proportion of their availability than any oak species (though none were apparently buried for future use).

Wild boar appear put on weight more rapidly with acorns than beech mast, and the females especially are said to prefer acorn to beech mast (Jones 1959). Henry and Conley (1972) in a study of wild boar introduced to the southern Appalachians also found an apparent preference for acorns over beech and hickory.

Smith and Scarlett (1987) noted that abundance of populations of woodpeckers and jays showed no correlations with crops of other masting species (hickories and walnuts in this study) supporting previous observations of lack of use of these hard-shelled nuts (with the possible exception of pecans, *C. illinoensis*) by birds.

Observations of apparent preferences must be treated with caution. For example, in Lewis' study the actual numbers of hickory nuts eaten were far smaller than acorns of any of the oaks, due to the small proportion of hickory trees present. Few mast species are as widespread as the oaks, or as abundant within the ecosystems within which they occur. It is also apparent from the studies described here that what has passed into the literature as preference is, in many cases, use of other genera earlier in the season, which may relate both to the sequence of ripening and to their relative keeping qualities; and neither of which preclude subsequent heavy use of the acorn crop.

4.4.6.5. Effects of crop size on utilization of acorns

As indicated in this Appendix, 4.4.2., 4.4.3, and throughout the preceding discussion, the size of the acorn crop may have a direct effect on some animal populations. Despite this, many animals are able to modify their feeding in response to acorn abundance. As indicated in the previous section, several studies examining the preferences of animals for different mast species have noted that use of the crop appears to correlate with availability rather than any other measure, which supports the proposition that most animals will focus on acorns if they are there and use something else if they are not, or, perhaps more importantly, if other foods are available in greater abundance.

Studies which note the apparently heavier use of acorns (of one species in relation to others, or as a whole in relation to other mast crops) in years of abundance include those of Davison (1964, and studies cited therein - see also this Appendix, 4.4.6.7.) and Eddy (1961). Smith and Follmer (1972) examined the feeding habits of squirrels and concluded that annual variation in mast production was possibly the most important factor determining the use of any particular food. Korschgen (1962) commented that, in the Ozarks, only in one year of drought, when other plants were in short supply, were acorns apparently over-used relative to their abundance. The quantity of acorns consumed also varied over the area studied, from the river valleys to the mountains, presumably in relation to acorn availability in these different regions. In a study of ruffed grouse utilization Korschgen (1966) noted heavy feeding in a good mast year, with acorn use remaining heavy until April, and continuing to some extent throughout the year, whereas in the following year of near crop failure acorns formed only a small part of the diet in the autumn, with a trace over winter. Servello and Kirkpatrick (1989) also commented on the greater proportion of acorns in the diet of this species when they are abundant. Others who found heavy use by some species in good mast years include Landers *et al.* (1977 - wood ducks); and Sork (1984) who found that losses to all animals could amount to more than 99% of acorns, even in a relatively large crop year.

One factor which might especially exacerbate losses from high-producing areas in relation to those from low-producing areas is the effects of mobile species. For example, Smith and Scarlett (1987) examined the effects of size of acorn crops on fluctuations of mast-eating birds, and found that some at least may react to changes in mast abundance on a local scale. It seems likely that migratory or mobile species may focus on areas or trees with heavy production, leaving less productive areas to suffer less heavy losses.

Despite this correlation of use with abundance, many studies have found greater percentage losses to wildlife in years of low productivity (e.g., Burns *et al.* 1954; Christisen 1951, 1955; Dalke 1953; Downs 1944; Downs and McQuilkin 1944), and the effects of animals focussing on other foods when acorns are not available, resulting in less use, is counter-balanced by the fact that smaller numbers were available in the first place; though the effects in years of intermediate production may be more difficult to determine. The study by Burns *et al.* examined differences in the total losses between good and poor years, and found the proportion of sound acorns remaining to be higher than average in abundant years for the red oaks, and about average in other oaks. Tryon and Carvell (1962) attempted to compare losses of acorns between good and poor years, but found the results too erratic to analyse. They also compared differences between high and low producers in one year, which might be expected to show the same relationship, but found them to be not significant. However, most studies indicate that acorns will disappear more rapidly in years when there are few of

them. These findings incidentally are what would be predicted by the seed-predator hypothesis (see Appendix 3, 3.3.2.4.), since in years of high productivity, despite increased use, the ecosystem should be saturated with acorns, so that there are more present than can possibly be eaten.

Perhaps the most important effect of varying acorn abundances is reflected by the length of time that acorns remain available in any one year. Griffin (1980a) noted that in poor years in California birds would remove most acorns (of *Q. lobata*) from the trees before they fell, while in good years, despite arboreal losses and the effects of insects, good acorns would accumulate on the ground in October and November. As long as deer and cattle were excluded most of these acorns remained on the ground until the pocket gopher became active in February, with acorns remaining on the ground until March or later. Others who have noted rapid disappearance of the crop in years of low production, or surpluses in good years include Downs (1944) and Korschgen (1962). Duncan and Clawson (1980) however, noted that even in a heavy-cropping year most acorns (of *Q. douglasii*) were eaten in the trees by ground squirrels. Koenig (1980) found that the acorn woodpecker harvested different species in different proportions each year, though he does not indicate whether this related to local production; and Koenig and Mumme (1987) found that this species was able to fill all storage holes in good years, but were not able to do so in many other years, especially acorn-poor years.

4.4.6.6. Other factors affecting acorn utilization

One factor that might affect the use of acorns is the ease of harvesting. Presumably there is a competitive advantage in being able to utilize acorns before other species do, but another reason for perhaps favouring unripe acorns is that it may be easier for some animals, particularly birds and squirrels, to carry off acorns when the cups are still attached, as they usually are not once the acorns have fallen. Ridley (1930) thought this to be the case especially in some tropical acorns, which, with their generally thicker shells, may require longer periods of manipulation, and which are sometimes covered with silky hairs, making them more difficult to grasp. Those acorns which remain in their cupules after they fall might also be favoured for similar reasons, though otherwise they would presumably be less preferred as it would require more effort to get into them.

Another factor that might influence the extent of use by vertebrates, is the amount of insect damage to acorns. Although there have been suggestions that some animals specifically target the nutritious insect larvae (Miller and Lamb 1985; Van Dersal 1940), others have noted that squirrels will carefully select their acorns, and reject many, possibly by estimating the weight of the kernel (Ridley 1930). Winston (1956) also observed grey

squirrels picking up and smelling acorns, and discarding those which contained insect larvae or fungi. Pekins and Mautz (1988) noted that deer may be selective against infested acorns. In cases of heavy insect damage there would be relatively fewer undamaged acorns available for selective animals to focus on.

Koenig and Mumme (1987) noted that the acorn woodpecker appears preferentially to store acorns of a particular size (1.2-1.4g), and this does not depend on the sizes available, or the species of acorn selected, which may vary considerably from year to year.

One advantage humans might have is in exploiting acorns is that their presence might also reduce the levels of acorn use by some animals. Bourne (1945, cited in Evans 1988) noted greatly reduced removals of acorns next to human habitation, with greatly increased removal some way beyond, returning to normal levels further away.

4.4.6.7. Preferences for acorns of different species

4.4.6.7.1. Feeding studies

Several studies have examined the ability of animals to digest acorns, again largely in North America (Baumgras 1944; Forbes *et al.* 1941; Havera and Smith 1979; Koenig and Heck 1988; Koenig 1991; Lewis 1982; Servello *et al.* 1987; Servello and Kirkpatrick 1987, 1989; Short 1976; Short and Epps 1976; Smallwood and Peters 1986; Smith and Follmer 1972; Sork 1984). Generally digestion of protein from acorns is poor, and studies have indicated that protein from other sources is required in a diet in which acorns are a large component. It is likely that this is largely due to the presence of tannins (see Appendix 2). The negative correlation between tannin concentration and digestibility of acorns has been proposed as explanation for apparent preferences for acorns of low tannin concentration (usually those of the *Lepidobalanus* group). Conversely, studies indicating preferences for acorns high in tannins, or for increased growth rates on diets of such acorns have generally been explained with reference to the higher fat concentrations found in acorns of the high tannin *Erythrobalanus* group.

Despite much effort put into field studies and experimental feeding trials on mammals and birds there is still no clear consensus regarding whether animals prefer high tannin/high fat acorns over low tannin/low fat. Short and Epps (1976) for instance, commented that acorns of red oaks were apparently less palatable to squirrels than those of white oaks, because of their higher concentration of tannins; while, conversely Smith and Follmer (1972) concluded tannins were not important in food preferences of squirrels. Koenig (1991) demonstrated adverse effects on digestibility of acorns by the acorn woodpecker when

tannins were added to an acorn diet, and beneficial effects when adding lipids. However, when both were added together the adverse effects of tannins were increased. There are evidently many potential complex interactions involved in digestibility, and different metabolic behaviour by different species certainly exists (compare the North American grey and European red squirrels, in this Appendix, 4.4.5.1.1.).

4.4.6.7.2. Observations in the wild

Apart from those nutritional studies which have examined experimentally the preferences of animals for acorns of different species there are also records of observations which have been made in the wild. Here the focus is on those aspects of preferential use which might indicate to what extent people might have to compete with other animals for particular species, or, conversely, to what extent some species might be less favoured by animals and might therefore be more readily available to people.

Van Dersal (1940), in a study of acorn utilization by North American wildlife, suggested that some oaks were more palatable or valuable than others (both as acorns or as leafy forage, or for other purposes) and presented recorded uses for all oak species, though he did not differentiate between the parts of the tree being used. Apart from the limited data set available at that time Van Dersal commented on the relatively qualitative nature of the evidence, and also on the fact that most of the records did not distinguish the particular species involved. Although many more studies have subsequently been undertaken this is still very much the case; especially as studies in North America have focussed not so much on preferences of animals for individual species, as on differential use of acorns of the red- and white- oak groups. Even on this topic little consensus has apparently been arrived at, though some general principles have emerged.

4.4.6.7.3. California and western North America

Several studies in this area have dealt with the acorn woodpecker, in particular the series of studies undertaken by Koenig and colleagues. One study (Koenig 1980) found that the numbers of each species of acorn stored by the acorn woodpecker varied from year to year, though the mean values over three seasons indicated that *Q. lobata* made up 33.7% of total stored acorns, *Q. douglasii* 30%, *Q. agrifolia* 16.9%, *Q. kelloggii* 13.8% and *Q. chrysolepis* 5.6%. In a continuation of this study (Koenig and Mumme 1987) *Q. douglasii*, *Q. agrifolia* and *Q. lobata* alternated position as the most abundantly stored species, the last in three years of six. *Q. lobata* was also the only species which was not nearly absent in at least one year. They do not present the averaged percentages stored over the longer study

period, but their histogram indicates that the order of importance remained the same, except that *Q. agrifolia* became the second most important species, and *Q. douglasii* the third.

Despite these findings, Koenig and Heck (1988) cited unpublished observations suggesting that the acorn woodpecker appears to prefer *Q. agrifolia* over other species in the field. One complication in studies of the acorn woodpecker is that those acorns stored only make up a small percentage of the total acorns consumed. Koenig and Heck suggested the apparent preference for acorns of *Q. agrifolia* may relate to its higher fat content, and therefore higher energy value, which might be of more importance for storage, especially since, for the acorn woodpecker, this is limited by the size of the granaries. The results of these studies are therefore rather inconclusive, though it seems likely that, as with the case of apparent preference for genera (see this Appendix, 4.4.6.4.) the relative abundance of acorns may be as important as any other factor. Other studies of the Acorn woodpecker by MacRoberts and MacRoberts (cited in Verner 1980) found that all acorn species available were used.

Regarding Californian wildlife use in general Barrett (1980) observed that acorns of all species but the tan oak (*Lithocarpus densiflora*) rapidly disappear once they have fallen. He presented data showing the recorded use by each animal species of individual oak species, indicating that the most commonly utilized acorns were of *Q. lobata* and *Q. wislizenii*, followed by *Q. kelloggii*, and *Q. agrifolia*. Other species were only positively recorded for one or two species. However, as discussed above, results of this kind should not be regarded as conclusive. Wolf (1945) found that in years of abundant crops pigs, cattle and sheep on a California ranch ate the acorns of *Q. garryana* first, and did not move onto the red oaks, *Q. kelloggii* and *Q. wislizenii* until they were finished. In another area, in a year of good production, he noted large numbers of *Q. kelloggii* acorns remaining on the ground, apparently unharvested by local animals.

One study of the collared peccary in southern Arizona showed greatest use of *Q. arizonica* (a white oak), followed by *Q. hypoleucoides*, with considerably smaller use made of *Q. emoryi* (both red oaks). Though the study only involved observations in one year, preference apparently related to acorn abundance, since the largest crop was produced by *Q. arizonica* (Eddy 1961).

4.4.6.7.4. Eastern North America

In this area there has been a particular focus on relative preference for white- or red-oak group acorns. The white oaks are frequently considered to be the preferred group, and it is often suggested that this is because they tend to be lower in tannin. This apparent

preference was generally confirmed by most earlier observations. White-oak acorns are still often cited as the preferred wildlife food in general literature.

Q. alba in particular is often cited as a highly preferred food by many types of wildlife (Martin *et al.* 1951, cited in Havera and Smith 1979), but it may well be that this relates as much to its widespread distribution as to any other factor. Van Dersal (1940), in his listing of recorded uses of oak species found 14 records for *Q. alba*, and only slightly fewer, 11, for *Q. rubra*, which has a similarly wide distribution.

The study by (and others cited in) Servello and Kirkpatrick (1989) on the ruffed grouse in the southeastern United States, have implied a preference for white-oak acorns; and similar studies of eastern North American squirrels have repeated the assertions that white-oak acorns are more palatable and that red-oak acorns are either ignored or eaten only after all white-oak acorns have been eaten (Dallen 1943, cited in Nixon *et al.* 1968; Havera and Smith 1979; Uhlig 1955, cited in Nixon *et al.* 1968; Uhlig 1956, cited in Davison 1964). However, acorns of both groups have been offered to grey squirrels and they have been fed on indiscriminately (Davison 1964; Nixon *et al.* 1968). Duvendeck (1962) noted an apparent preference by white-tailed deer for *Q. alba* over *Q. rubra*, but found no differences in body weight when they were fed on one or the other. Observations made by Burns *et al.* (1954), Downs and McQuilkin (1944) and Korstian (1927) showed no apparent preferences by wildlife for acorns of either oak group.

Those studies which have examined utilisation in the field have generally indicated that species are used according to their abundance (as discussed in this Appendix, 4.4.6.5. and, in relation to other mast-producing trees, in 4.4.6.4.). For example, Korschgen (1962) examined consumption over 5 years by white-tailed deer of 11 species of a mixture of red and white oaks in Missouri. He found that *Q. velutina* was the most important followed by *Q. rubra*, *Q. alba*, *Q. stellata* and *Q. coccinea*, *Q. marilandica* and *Q. palustris*, but that preference seemed to correlate most closely with abundance in any one year, and there was no noticeable preference for red or white oaks - deer fed on what was available. In a similar study of squirrels he found a similar pattern of consumption (Korschgen 1981), and in two further studies he noted heavier use of the acorns of red oaks by ruffed grouse, again in relation to their greater abundance (Korschgen 1966). Barber (1954, cited in Davison 1964), has also noted the utilisation of oak species (and other mast trees) in relation to their abundance.

One of the facts cited as evidence for greater palatability of white-oak acorns is the fact that they tend to remain on the ground for less time than red-oak acorns (see 4.5., below). It seems likely that many studies in the field indicating preference for acorns of the white oaks

relate to the time of observation. Acorns of the white-oak group tend to germinate soon after they mature, sometimes before the onset of winter, and tend to be primarily a food of autumn and winter (5.3.3.; Havera and Smith 1979; Short and Epps 1976); while red-oak acorns, have better keeping qualities, and therefore are often the favoured food over winter, by which time the white-oak acorns have been eaten. Petruso and Wickens (1984) observed that acorns of *Q. alba* and *Q. prinus* in Indiana fell earliest and were eaten immediately, and it was not until mid-November that animals began to eat acorns of the red oaks. However, this does not mean that they are not eventually used. One study was undertaken by Sork (1984), who attached metal tags to *Q. rubra* acorns, and found that they had a very low survival value. She estimated that animals ate, or removed elsewhere, more than 99% of the acorns, even in a year with a relatively large crop.

Further support for this suggestion is provided by the study by Tryon and Carvell (1962) who examined use of acorns in northern West Virginia over five years and found that damage to acorns on the tree was greater for *Q. alba* than for *Q. rubra* (26.1% vs. 13.1%), while on the ground it was greater for *Q. rubra* than *Q. alba* (32.5% vs. 25.5%). The total losses to animals however were very similar, comprising from 53.2% to 58.6% of the *Q. alba* crop, and 50.2% of the *Q. rubra* crop. Data on percentage losses of acorns of different species to animals are shown in Table 16, and further discussed in Chapter 7.

The potential effect on their utilisation of the better storage qualities of red-oak acorns is indicated by the study of Lewis (1982). He found a greater proportion of the available *Q. rubra* crop buried in late autumn samples (19% of those available) than of either *Q. prinus* or *Q. alba* (both less than 1.5% of those available). The largest numbers of acorns eaten over winter were those of *Q. prinus* (a white oak), followed by *Q. rubra* (comprising together 90% of the total). Lewis suggests that, in fact, squirrels are showing a preference for red over white-oak acorns, as, relative to their availability there was again a preference for *Q. rubra* (3.8%) (after *Carya glabra* - 9.7%), then *Q. prinus* (1.9%) then *Q. alba* (0.3%).

Scarlett and Smith (1991) observed that blue jays preferentially selected acorns of the red-oak group. These acorns were stored by the jays and they suggested that the storage requirement influenced this preference. The jays also showed a strong preference for species with small acorns.

4.4.6.7.5. Europe

Very little work has been done on relative preferences for acorn species in other parts of the world. In northern Europe introduced grey squirrels have been reported to show some

preference for acorns of *Q. petraea* rather than *Q. robur*, but it is apparently possible to find some trees untouched adjacent to others of the same species where all acorns have been eaten by squirrels (Corbet 1974). Parsons (1962) notes that pigs find acorns of *Q. ilex* more palatable than those of *Q. suber*.

Hadfield (1974) found that acorns of *Q. robur* were apparently more attractive to arboreal-feeding birds, and suggested that this was because their long peduncle makes them easier to harvest and carry away from trees.

4.5. PERIOD OF AVAILABILITY OF ACORNS

Variations in the length of time that acorns are available could be an important factor in their utilisation by people. In Appendix 3, 3.2.7., variations in the time of acorn fall have been discussed. However, acorns may be used by animals both before and after this (see this Appendix, 4.4.6.1.).

Acorns are apparently acceptable to many animals in an under-ripe state, as the numbers of species reported to eat acorns from the trees demonstrates. There is little discussion in the literature regarding the time at which acorns become acceptable food to animals (see 6.4.1.), but though most feeding in the trees probably involves almost ripe acorns, just before or during the time of acorn drop, some may apparently be eaten while still quite green. Acorn woodpeckers eat "green" acorns fresh from the trees from early August until October, and sometimes as late as December, while acorns are collected for storage from early September until early March (though mainly from October to December) (Koenig and Mumme 1987; Verner 1980). Wood (1938) recorded grey squirrels harvesting acorns in August, by notching cups and removing the acorns.

As noted in Appendix 3, 3.2.7., there is a considerable range in the time during which acorns may remain on the trees. Some trees retain their acorns for longer periods than others, and Koenig and Mumme (1987), in California, found that retention of acorns late into winter and even spring was highly variable. Some species seemed to retain some of their acorns longer than others, and in some years considerable numbers of the evergreen species still bore acorns as late as March, and in one year, following a bumper crop, as late as June, over a considerable area.

Acorns are obviously at their most abundant during the period of drop, but they may persist on the ground and continue to be a valuable food for wildlife for some time. The period of availability of acorns on the ground is dependent upon several factors, including the oak species present, period of acorn drop, size of crop, and extent of predation. For example,

in one year in Arizona Eddy (1961) found that the collared peccary was able to eat acorns for most of the year, feeding on *Q. emoryi* from July to September, *Q. hypoleucoides* from October to December, and *Q. arizonica* from October to March (in a year when the latter produced an abundant crop). In the east Nixon *et al.* (1968) found that squirrels used acorns throughout the year; and in a study area with at least seven oak species present Korschgen (1962, 1966) found that acorns were usually available to non-storing species from September until May, and sometimes throughout the year. Watt (1919) found that viable acorns of *Q. petraea* and *Q. robur* could remain on the ground ungerminated as late as the summer especially in dry years, and Jensen (1982) noted a similar situation in Central Europe and Southern Scandinavia. Even the cotyledons of germinated acorns may be eaten by animals through summer and autumn of the year following their dispersal (Bosema 1979, cited in Fenner 1985; Wood 1938).

The period of availability of acorns may vary from year to year. Downs and McQuilkin (1944) present a graph showing such variations, for five species combined, over several years. The period for which acorns remained available varied from early November to February and beyond, and appeared to be related to crop size. Korschgen (1966) also found that though acorns might often be available all year, in poor years they could all be gone by November. Such annual variation, together with variation between different areas, is largely dependent upon the often complex interactions between acorn crop size, presence of different animal species, and their population densities, as has been discussed (see, e.g., Appendix 3, 4.4.6.5.).

It is often said that the period of availability of acorns in North America varies according to the oak group to which they belong (see this Appendix, 4.4.6.7.), and that this relates to a supposed preference by wildlife for white-oak acorns; though it is more likely that red-oak acorns tend to remain edible for longer periods, largely because white-oak acorns germinate earlier (see 5.3.3. and this Appendix, 4.4.6.7.). Their is surprisingly little quantitative data regarding the period of availability, and what data are available suggests that acorns of either group may be fed on intensively during the period of maximum availability (see also Table 16). Petruso and Wickens (1984) undertook a study to compare the period of persistence on the ground of three species. They found acorns of *Q. alba* and *Q. prinus* available in maximum numbers around October 15th, with the former persisting in considerable numbers for at least three weeks (by which time many had begun to sprout), and declining slowly through December; while the latter declined rapidly within two weeks of the peak period, and then more slowly to the end of November. Numbers of fallen *Q. rubra* acorns did not peak until October 25th, and numbers of acorns on the ground declined slowly until January and beyond. This was particularly so in the case of trees occupying isolated positions. The findings were supported by other observations of acorns

of red-oak acorns under trees until early February. This study, however, took place during only one year, and it may not indicate a general trend. As suggested in this Appendix, 4.4.6.7., on some occasions red-oak acorns may disappear as rapidly as those of white oaks, and white-oak acorns may remain available for considerable periods. Korschgen (1962), for instance, found that deer were still feeding on *Q. alba* acorns as late as the summer.

4.5.1. Effects of variations in animal abundance

One other factor of importance in both the total losses of acorns and the time during which acorns remain on the ground are variations in abundance of animals, with rapid disappearance of crops when there are high animal numbers, and surpluses when there are not (e.g., Christisen 1951; Downs 1944). Downs noted that, while even when there were only light animal populations most of a light crop was consumed, with large animal populations practically the entire crop would be consumed, except in years of heavy production. The potential for rapid disappearance of a crop when there are high animal population densities is shown by one study in which an exceptionally heavy fall of acorns of *Q. kelloggii* occurred at the beginning of October. By October 20th 85% had disappeared, and all had gone by the end of November. In this case a very heavy deer population was largely responsible (Bowyer and Bleich 1980).

1. Western North America							
Species	Condition of Acorns (% of developed acorns)					Comments	Source
	Aborted	Developed					
		Insect/ fungi damaged	Damaged/eaten by birds/mammals		Sound		
			On trees	On ground			
Erythrobalanus							
Q. agrifolia	—	22	—	—	[78]	6 yrs., from acorn woodpecker granaries	Koenig & Mumme 1987
Q. kelloggii (mainly)	—	—	85		[15]	by Oct. 20th, 94% of these by deer, yr. of heavy crop & high deer numbers; S. California	Bowyer & Bleich 1980
	—	20	—	—	[80]	6 yrs., from acorn woodpecker granaries	Koenig & Mumme 1987
	—	few	—	—	—	at time of drop	Wolf 1945
Lepidobalanus							
Q. douglasii	—	—	most	few	few	heavy crop, ground squirrels in trees, deer	Duncan & Clawson 1980
	—	36	—	—	[64]	6 yrs., from acorn woodpecker granaries	Koenig & Mumme 1987
Q. garryana	—	v. few	—	—	—	at time of drop	Wolf 1945
Q. lobata	—	(0)-21-(31)	some-most	—	few-many	different yrs., largely dependent on crop size	Griffin 1980a
	—	—	—	nearly all	very few	as previous, of sound acorns, by Jan.	"
	—	—	—	66-100	0-44	as previous, by March, deer & cattle excluded	"
	—	42	—	—	[58]	6 yrs., from acorn woodpecker granaries	Koenig & Mumme 1987
	—	15	—	—	—	of "sound" acorns collected and spread to dry several weeks	Wolf 1945
Protobalanus							
Q. chrysolepis	—	32	—	—	[68]	6 yrs., from acorn woodpecker granaries	Koenig & Mumme 1987
Quercus spp. "All but [*Lithocarpus densiflorus*]"	—	—	—	Up to 100	[0+]	rapidly disappear, greatest loss where deer, feral pig or bear occur	Barrett 1980
Quercus spp.	—	≤80	—	—	[20]	acorns collected by foresters	Brown 1980
Quercus spp.	—	most	—	—	few	acorns falling before Oct.; Carmel Valley, California	Griffin 1971
Quercus spp.	—	13/53	—	—	—	max. and min. annual loss, 5 spp. combined, over 6yrs., from acorn woodpecker granaries	Koenig & Mumme 1987

Table 16. Losses from the acorn crop (continued over)

2. Eastern North America							
Species	Condition of Acorns (% of developed acorns)					Comments	Source
	Aborted	Developed					
		Insect/ fungi damaged	Damaged/eaten by birds/mammals		Sound		
			On trees	On ground			
Erythrobalanus							
Q. coccinea	30-45	48-70	10-16		14-42	Aug. - Dec., range of 2 sites, 6 yrs; Missouri Ozarks	Burns *et al.* 1954
	16	56	4		41	one yr.; Missouri	Dalke 1953
	103	31	12	—	57	at drop, mean 7 yrs; Bent Creek, S. Appalachians	Downs & McQuilkin 1944
	90	31	23	—	46	at drop, mean 7 yrs; Toccoa, S. Appalachians	"
	—	2	—	—	—	"sound" acorns after cutting tests, 2 sites; North Carolina	Korstian 1927
Q. falcata	—	18	—	—	82	at drop, mean 18 yrs; Louisiana/Texas	Goodrum *et al.* 1971
Q. incana	—	26	—	—	74	at drop, mean 6 yrs; Louisiana/Texas	"
Q. marilandica	45-85	60-71	15-19		14-21	Aug. - Dec., range of 2 sites, 6 yrs; Missouri Ozarks	Burns *et al.* 1954
	29	60	4		36	one yr.; Missouri	Dalke 1953
	57	72	0		29	next yr.; Missouri	"
	—	27	—	—	73	at drop, mean 18 yrs.; Louisiana/Texas	Goodrum *et al.* 1971
Q. nigra	—	30	—	—	70	at drop, mean 6 yrs.; Louisiana/Texas	"
Q. palustris	70	26	16		58	at drop, 12 yrs., two sites; Southeastern Missouri	McQuilkin & Musbach 1977
	—	33	—	—	67	as previous, natural area	"
	—	16	—	—	84	as previous, artificially-flooded	"

Table 16. Losses from the acorn crop (cont.)

Species	Condition of Acorns (% of developed acorns)					Comments	Source
	Aborted	Developed					
		Insect/ fungi damaged	Damaged/eaten by birds/mammals		Sound		
			On trees	On ground			
Q. rubra	9	34	1		65	one yr.; Missouri	Dalke 1953
	50	67	33		0	next yr.; Missouri	"
	116	23	21	—	57	at drop, mean 7 yrs.; Bent Creek, S. Appalachians	Downs & McQuilkin 1944
	74	25	30	—	45	at drop, mean 7 yrs.; Toccoa, S. Appalachians	"
	—	47	8		45	Sept. - Dec., 5 yrs., good site; S. Michigan	Gysel 1957
	140	28	65		8	March/April, one tree; North Carolina	Korstian 1927
	—	5-27	—	—	—	range of 3 sites, incs. "sound" acorns, after cutting tests; North Carolina & Connecticut	"
	—	—	—	55-95	5-45		Krajicek 1955 (in Tryon & Carvell 1962)
	—	—	—	>99	<1	of metal-tagged acorns; Missouri	Sork 1984
	—	35	13	37	14	Sept. - April, 14 trees, 5 yrs., "on trees" figure is for acorns removed; Ozarks	Tryon & Carvell 1962
Q. velutina	11-61	46-72	7-13		16-41	Aug. - Dec., range of 3 sites, 6 yrs.; Missouri Ozarks	Burns *et al.* 1954
	20	71	2		27	one yr.; Missouri	Dalke 1953
	84	77	19		4	next yr.; Missouri	"
	199	42	32	—	26	at drop, mean 7 yrs.; Bent Creek, S. Appalachians	Downs & McQuilkin 1944
	153	32	48	—	20	at drop, mean 7 yrs.; Toccoa, S. Appalachians	"
	—	35	13		52	Sept. - Dec., 5 yrs., medium site; S. Michigan	Gysel 1957
	—	29	47		24	Sept. - Dec., 5 yrs., poor site; S. Michigan	"
	5	29	71		<1	March/April, 9 trees; North Carolina	Korstian 1927
	—	46	—	—	—	"sound" acorns, after cutting tests, one site; North Carolina	"
	—	28	—	—	[72]	of 255 planted acorns, destroyed by weevils; New Jersey	Wood 1938

Table 16. Losses from the acorn crop (cont.)

Species	Condition of Acorns (% of developed acorns)				Comments	Source
	Aborted	Developed				
		Insect/ fungi damaged	Damaged/eaten by birds/mammals	Sound		
			On trees / On ground			
Lepidobalanus						
Q. alba	6-37	57-72	11-22	14-32	Aug. - Dec., range of 3 sites, 6 yrs.; Missouri Ozarks	Burns *et al.* 1954
	36	98	<1	2	one yr.; Missouri	Dalke 1953
	76	68	26	6	next yr.; Missouri	"
	165	49	29 —	22	at drop, mean 7 yrs.; Bent Creek, S. Appalachians	Downs & McQuilkin 1944
	159	15	22 —	63	at drop, mean 7 yrs.; Toccoa, S. Appalachians	"
	—	9	— —	91	at drop, mean 5 yrs.; Louisiana/Texas	Goodrum *et al.* 1971
	—	56	17	27	Sept. - Dec., 5 yrs., good site; S. Michigan	Gysel 1957
	—	48	18	34	Sept. - Dec., 5 yrs., medium site; S. Michigan	"
	12	7	93	1	Nov., one tree, North Carolina	Korstian 1927
	2.0	11+2	74	14	March/April, 12 trees, + is germinating acorns; North Carolina	"
	—	0-15	— —	—	range of 3 sites, incs. "sound" acorns, after cutting tests; North Carolina/Connecticut	"
	—	30	26 33	12	Sept. - April, 14 trees, 5 yrs., "on trees" figure is for acorns removed; Ozarks	Tryon & Carvell 1962
	—	7	— —	[93]	of 255 planted acorns, destroyed by weevils; New Jersey	Wood 1938
Q. bicolor	—	21	— —	—	after cutting tests, one site; N. Carolina	Korstian 1927
Q. macrocarpa	—	55	— —	—	after cutting tests, one site; N. Carolina	"
Q. michauxii	—	6	— —	94	at drop, mean 4 yrs.; Louisiana/Texas	Goodrum *et al.* 1971
	—	0	— —	—	after cutting tests, one site; N. Carolina	Korstian 1927

Table 16. Losses from the acorn crop (cont.)

Species	Condition of Acorns (% of developed acorns)					Comments	Source
	Aborted	Developed					
		Insect/ fungi damaged	Damaged/eaten by birds/mammals		Sound		
			On trees	On ground			
Q. prinus	24	50	25	—	25	at drop, mean 7 yrs.; Bent Creek, S. Appalachians	Downs & McQuilkin 1944
	29	18	21	—	61	at drop, mean 7 yrs.; Toccoa, S. Appalachians	"
	5	10+5	78		7	March/April, several trees, + is germinating acorns; N. Carolina	Korstian 1927
	—	1	—	—	—	"sound" acorns, after cutting tests, Connecticut	"
	—	8	—	—	[92]	of 255 planted acorns, destroyed by weevils; New Jersey	Wood 1938
Q. stellata	104-127	80-87	8		5-12	Aug. - Dec., range of 2 sites, 6 yrs.; Missouri Ozarks	Burns *et al.* 1954
	335	50	49		1	by Dec. 15th, vary with abundance of acorns and wildlife; Missouri	Christisen 1951
	141	94	2		5	one yr.; Missouri	Dalke 1953
	64	82	8		10	next yr.; Missouri	"
	—	28	—	—	72	at drop, mean 18 yrs.; Louisiana/Texas	Goodrum *et al.* 1971

Table 16. Losses from the acorn crop (cont.)

Species	Condition of Acorns (% of developed acorns)					Comments	Source
	Aborted	Developed					
		Insect/ fungi damaged	Damaged/eaten by birds/mammals		Sound		
			On trees	On ground			
Quercus spp. (*Erythrobalanus* spp. combined)							
	11-85	46-72	7-19		14-42	range of 3 spp., 6 yrs; Missouri Ozarks	Burns *et al.* 1954
	—	—	26-54	5 (per day)	[<46-<74]	Sept. - Nov., range of 3 yrs.,*Q. nigra* & *Q. phellos*, mostly jays & woodpeckers, incs. 12.8-13.8% removed from trees; Arkansas bottomlands	Cypert & Webster 1948
	9-29	34-71	1-4		27-65	range of 4 spp., one yr; Missouri	Dalke 1953
	50-84	67-77	0-33		0-29	as previous, excluding 1 sp., following yr.	"
	9-84	34-77	0-33		0-65	as previous, range of 2 yrs.	"
	103-199	23-42	12-32	—	26-57	at drop, range of 3 spp., 7 yrs., Bent Creek; S. Appalachians	Downs & McQuilkin 1944
	74-153	25-32	23-48	—	20-46	at drop, range of 3 spp., 7 yrs., Toccoa; Southern Appalachians	"
	74-199	23-42	12-48	—	20-57	as previous, range of 2 sites	"
	—	29-47	8-47		24-52	range of 2 spp., Sept. - Dec., 5 yrs.; S. Michigan	Gysel 1957
	5-14	28-29	64-71		<1-8	range of 2 spp., March/April; North Carolina	Korstian 1927
	—	2-46	—	—	—	"sound" acorns, range of 3 spp., after cutting tests, Connecticut & North Carolina	"

Table 16. Losses from the acorn crop (cont.)

Species	Condition of Acorns (% of developed acorns)				Comments	Source
	Aborted	Developed				
		Insect/ fungi damaged	Damaged/eaten by birds/mammals		Sound	
			On trees	On ground		
Quercus spp. (*Lepidobalanus* spp. combined)						
	6-127	57-87	8-22		5-32	range of 2 spp., 3 sites, 6 yrs.; Missouri Ozarks	Burns *et al.* 1954
	36-141	94-98	<1-2		2-5	range of 2 spp. one yr.; Missouri	Dalke 1953
	64-76	68-82	8-26		2-10	as previous, following yr.	"
	36-141	68-98	<1-26		2-10	as previous, range of 2 yrs.	"
	24-165	49-50	25-30	—	22-25	at drop, range of 2 spp., 7 yrs., Bent Creek; S. Appalachians	Downs & McQuilkin 1944
	29-159	15-18	21-22	—	61-63	at drop, range of 2 spp., 7 yrs, Toccoa; Southern Appalachians	"
	24-165	15-50	21-30	—	22-63	as previous, range of 2 sites	"
	—	82+17	—	—	1	May 20th, sample apparently sound at drop, completely + partially destroyed	"
		94+6	—	—	0	as previous, sample obviously infested at drop	"
	2-5	13-15	74-78		7-14	range of 2 spp., March/April; North Carolina	Korstian 1927
	—	0-55	—	—	—	"sound" acorns, range of 5 spp., after cutting tests, Connecticut & North Carolina	"

Table 16. Losses from the acorn crop (cont.)

Species	Condition of Acorns (% of developed acorns)					Comments	Source
	Aborted	Developed					
		Insect/ fungi damaged	Damaged/eaten by birds/mammals		Sound		
			On trees	On ground			
Quercus spp. (both subgenera combined)							
	6-127	46-87	7-22		5-42	Aug. - Dec., range of 5 spp., 3 sites, 6 yrs.; Missouri Ozarks	Burns *et al.* 1954
	9-141	34-98	<1-4		2-65	range of 6 spp., one yr.; Missouri	Dalke 1953
	50-84	68-82	0-33		0-29	as previous, 5 spp., following yr.	"
	9-141	34-98	0-33		0-65	as previous, range of 2 yrs.	"
	24-199	23-50	12-32	—	22-57	at drop, range of 5 spp., 7 yrs., Bent Creek; S. Appalachians	Downs & McQuilkin 1944
	29-159	15-32	21-48	—	20-63	at drop, range of 5 spp., 7 yrs., Toccoa; Southern Appalachians	"
	(24)-115-(199)	(15)-30-(50)	(12)-24-(48)	—	(20)-46-(63)	as previous, range and mean of 2 sites	"
	—	—	—	76	24	of sound acorns, March, one yr., Toccoa	
	—	—	—	few-most	few-fair surplus	of sound acorns, light deer populations, light and good crops	"
	—	—	—	<total crop	—	as previous, heavy deer population, all but heaviest crop yrs	"
	—	21	—	—	79	at drop, mean 7 spp.,4-18 yrs.; Louisiana/Texas	Goodrum *et al.* 1971
	—	—	some	most-all	—	as previous study site, 10 spp., of sound acorns, by end of drop, average crop yr.	"
	—	—	—	—	surplus	as previous, bumper crop yr.	"
	—	29-56	8-47		24-52	range of 3 spp., Sept. - Dec., 5 yrs.; S. Michigan	Gysel 1957
	—	60	—	—	[40]	of 280 mixed acorns, stored 3-4 weeks, both with & without wood ashes (99% of Lepidobalanus kernel destroyed, 50% Erythrobalanus)	Hilliard 1986

Table 16. Losses from the acorn crop (cont.)

Species	Condition of Acorns (% of developed acorns)					Comments	Source
	Aborted	Developed					
		Insect/ fungi damaged	Damaged/eaten by birds/mammals		Sound		
			On trees	On ground			
Quercus spp. (both subgenera combined - continued)	—	0-55	—	—	—	"sound" acorns, range of 8 spp., after cutting tests, Connecticut & North Carolina	Korstian 1927
	53	33	18	36	14	Sept. - April, 28 trees, 5 yrs., "on trees" figure is for acorns removed; Ozarks	Tryon & Carvell 1962
	—	39	10	43	9	as previous, trees with high production	"
	—	25	34	35	6	as previous, trees with low production	"
	—	—	9-50	—	50-91	estimated from no.'s empty cupules; New Jersey	Wood 1938
	—	4	—	71	17	of fallen acorns in previous; remainder mouldy or desiccated	"
	—	—	—	87	[13]	as previous, one year after drop, large herbivore population	"
3. Europe							
Q. petraea	—	8/30	—	—	—	two adjacent trees	Jones 1959
Q. robur	—	11/50	—	—	—	two adjacent trees	"
Quercus spp.	—	≤25	—	—	[75+]	good yr., appear to attack *Q. robur* and *Q. petraea* equally	"
Quercus sp.	—	—	54		—	removed and stored by jays	Darley-Hill & Johnson 1981 (in Fenner 1985)
	—	—	≤99		1+	small mammals and wood pigeons	Shaw 1968 (in Evans 1988)
	—	—	8-92	some	[<8-<92]	wood pigeon, rodents; Monks Wood, U.K.	Tanton 1965 (in Corbet 1974)
	—	—	10		90	yr. of maximum crop, mice, bank voles, jays, squirrels, latter may eat more from trees in low crop yrs.	Turcek 1967 (in Corbet 1974)

Table 16. Losses from the acorn crop (concluded)

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